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MONOCOTYLOUS SEEDLINGS

MORPHOLOGICAL STUDIES IN THE
POST-SEMINAL DEVELOPMENT
OF THE EMBRYO

BY

LUCY BOYD, D.Sc.

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I. INTRODUCTION.

Research on the Embryo and Seedling of Monocotyledons: Aims and Scope of the Present Investigation.

Early publications on seedlings, such as those of Irmisch, Klebs (1881–85), and the later work of Lubbock (1892), dealt entirely with external morphology. Hanstein's research (65) was one of the earliest microscopic investigations of the embryonic structure. Interest in the theory of stelar evolution focussed attention later on the vascular anatomy of the ripe embryo and seedling. Van Teighem (145) about 1870 reduced the transition anatomy of the seedling to three types. Compton (33) has summarised later research on seedlings from this standpoint. Theories on the vascular anatomy have been made by Gérard (60), Gravis (62), Schoute (129, 130), Jeffrey (84), Chauveaud (28, 29), and Bugnon (18, 19). The recent work of Chiarugi (30) and Messēri (102) in this connection may also be referred to.

At the beginning of the century seedling anatomy became the basis for phylogenetic theories. Impetus was given to the study by the work of Sargant, who proposed a new theory of the origin of the single-seed leaf of Monocotyledons. Her method consisted in comparing the anatomy of seedlings at the same stage of development and belonging to different genera and species, chiefly of Liliaceae. The record of her principal investigation is almost entirely confined to anatomical data. Her observations were extended by other botanists to Dicotyledons and Gymnosperms. Peculiarities in form and development were particularly the subject for discussion (47, 68, 141). Save for the researches of Gatin (1904–21) little has been done towards extending Sargant's studies to all families of Monocotyledons.

In 1915 Sargant and Arber published a memoir linking up the morphology of the embryo and seedling of Gramineae with that of other Monocotyledons. Since that date many papers on seedling anatomy have dealt with this subject. The studies in embryogeny by Souéges include certain

Monocotyledons (137), but modern research on the embryo is increasingly directed to its cytological aspects.

The principal aim of the present research was to add to the knowledge of the germination, external morphology, and anatomy of the seedling of Monocotyledons. A subsidiary aim was to discover to what extent a correlation existed between the seedling structure and habit of the adult plant. The data from the investigation of the material were first arranged according to family, but it was finally decided that, for the purpose of keeping the secondary aim of the investigation in sight, the habit of the adult plant would make a more satisfactory basis for classification. Certain plants, particularly members of the rhizomatous group, presented some difficulty. Where, for example, the plant is both climbing in habit and tuberous, or xerophytic and rhizomatous, it is placed in the section the members of which it most closely resembles. Although certain species of the Commelinaceae are annuals, morphologically they differ so little from the rhizomatous type that it was thought unnecessary to make a separate group of annual plants. Terrestrial and obligate epiphytic forms of Bromeliaceae are, for the sake of easy comparison, described in the same section. The embryo and seedling of Gramineae, which have raised such controversy in the past, merit separate discussion, which is followed by an account of the family showing closest affinity—the Cyperaceae.

No account is given of the Orchidaceae ; the examination of seedlings of a few genera does not justify the inclusion of the family in the present publication.

For the sake of adding to the scope of the survey, reference has been made whenever possible to the findings of previous workers.

Terminology.

The nomenclature for parts of the seedling is that at present in general use.

Types of Germination.—Extension in length of the embryo, usually of a zone of cotyledon tissue between the sheathing base and sucker, results in the rupture of the testa by the pushing forward of the primary root, which as a rule is the first organ of the seedling to emerge. For descriptive purposes three types of germination are differentiated.

Type A.—The radicle and base of the cotyledon grow vertically downwards. The elongating zone of cotyledon, which caused their emergence, increases in length, resulting in arching up of the cotyledon above the surface. The cotyledon consists of a short base, the plumular bud merging into a photosynthetic region, the *lamina* or blade, which may be cylindrical or flattened and tapers to the suctorial tip bearing the seed. As the endosperm is exhausted and growth proceeds, the cotyledon becomes erect, and the remains of the seed drop from the tip. The first leaf emerges towards the base of the cotyledon, through a lateral slit which may be surrounded by a low parenchymatous rim.

Type B.—The cotyledon is a subterranean organ. It consists of a sheathing base protecting the plumule, an intermediate sheathing region the elongation of which is responsible for propelling the radicle and cotyledon base deeper into the soil, and a narrower region, conveniently though not very happily designated *stalk*, equivalent to Velenovsky's (150) "Mittelstück," which passes into the suctorial tip in the seed. The first leaf emerges laterally or at the apex of the sheath, where it narrows into the stalk. A short non-vascular sheath, tubular or open, may form a margin around the cotyledon slit before the first leaf emerges.

Type C.—Germination is hypogeal. Extension of the same zone in the embryo propels the radicle and base of the cotyledon through the micropyle, but its elongation is more limited, hence the stalk connecting the sucker in the seed with the remainder of the cotyledon is usually short. At first the axis of the plantlet outwith the seed is not directed vertically downwards, but at an obtuse angle to the axis of the sucker. One or more days after the emergence of the radicle and sheathing base of the cotyledon, tissue on the upper side of the sheathing base arches up to form a hood which elongates during the early growth of the young leaves. The organs then assume their final orientation, the hooded plumular bud and the radicle being in vertical alignment at right angles to the cotyledon sucker, which increases in volume by the expansion of its cells. The first leaf escapes through a small pore or slit towards the apex of the hood or sheath. The latter, which may be short or of considerable length, has been termed a *ligule*. In most genera it is stiffened by vascular

tissue. For the sake of distinction, the designation has not in the present work been extended to the short non-vascular sheath associated with Type B. As far as the writer knows, Gatin first used the term in this connection in 1906. Sargant and Arber in 1915 preferred the expression "upper sheath" for it. In *Brachychilum* they termed it "the sheath," presumably because there was no lower sheath. The word "ligule" is a somewhat unfortunate choice. While a single word is preferable to the expression "upper sheath" or Gatin's "gaine ascendante," the term already has other associations in connection with the foliage leaf.

The *first leaf*, in the present work, means the first foliar organ produced from the plumular bud, even if it is of the nature of a scale leaf. The insertion of the base of the cotyledon on the main axis of the seedling, a level at which the cotyledon strands usually join the downward trace from the plumule, marks the upper limit of the *hypocotyl*. When the cotyledon strands enter the stele at different levels, the lowermost fusion is taken to be its upper limit. The lower limit is usually indicated by the formation of a typical root stele.

In spite of Arber's (2) criticism of this method as leading to "the fundamental error of treating the root stele as made up of cotyledonary and plumular strands," Sargant's convention of describing the anatomy from the cotyledon to the root has been followed in the present work for the sake of simplicity. In certain instances the anatomy of the transition from stem to root structure is referred to van Teighem's three types (145) to which Sargant added a fourth, the Anemarrhena type (118).

In referring to species the writer has adhered throughout to the nomenclature of the "Index Kewensis."

Methods.

Seeds were usually sown in soil at a suitable depth and germinated in a greenhouse. The seedlings were collected at stages from a day to several weeks old. In isolated cases observations were continued for one or two years. After fixation in Carnoy's Reagent the seedlings were dehydrated and transferred through graded mixtures of absolute alcohol

and chloroform to pure chloroform, in which they were immersed from twelve to twenty-four hours. Paraffin wax (m.p. 50° C.) was then gradually added in the cold. Chloroform was used as a solvent in preference to xylol as being more easily detected if present before embedding. The seedlings remained in paraffin at 51° for a period from one to three days. The length of time allowed for the penetration of chloroform, and later paraffin, was compensated for by certainty of results. Longitudinal and transverse sections, 10 μ in thickness, were prepared for each stage of development examined, stained with a mixture of 1 per cent. safranin in water and 1 per cent. safranin in alcohol, and counterstained with 1 per cent. light green in clove oil. For confirmatory purposes, the gross anatomy was occasionally followed in seedlings which had been dehydrated and cleared in xylol.

II. DESCRIPTION OF SEEDLINGS EXAMINED.

Hydrophytic and Helobic Types.

APONOGETONACEAE—*Aponogeton abyssinicus.*

The seed (fig. 1, i) is non-endospermic. The embryo, about 1 mm. long at maturity, is straight, spindle-shaped, and protected by an outer delicate, transparent, and an inner reddish-brown seed coat. The clearly differentiated radicle has a conspicuous root cap. The plumular bud develops laterally above the radicle, the second and third foliage leaves being differentiated before germination. The bulk of the embryo consists of cotyledon, the closely packed cells of which are filled with small, elliptical starch grains. A single vascular strand of undifferentiated meristem runs centrally down the cotyledon to the primary root, being joined by a weak plumular trace.

Germination (fig. 1) is epigeal. The radicle emerges at the micropylar end of the seed, and a ring of root hairs arises on a collar of tissue immediately behind the root tip and below the level of the plumule. An adventitious root which makes its appearance above the root hairs on the side remote from the cotyledon keeps pace in development with the plumule. The cotyledon does not become erect ; it consists for the most part of an isobilateral equitant blade, connecting tip and short sheathing base, but is originally cylindrical. The tip and much of the " blade " remain underground, possibly to assist in fixation. In older seedlings the sheath of the cotyledon is prolonged above the plumular bud into two sheath wings. The primary root continues to elongate for some time. During the first four or five weeks a small spherical corm-like body develops at the base of the plumular axis, an indication of the tuberous stem of the adult (fig. 1, v).

Anatomy (fig. 2). (i) *Seedling a Few Days Old.*—The single cotyledon strand is enclosed in a thin-walled sheath, and lies in a compact tissue placed between two aerenchymatous regions. Its stele does not increase to any extent in size or complexity, but the inner tangential wall of the sheath

thickens and the ground tissue becomes more aerenchymatous. The first leaf resembles the cotyledon in shape and in the distribution of aerenchyma, but has, in addition, two lateral strands. The traces from the plumular bud and first foliage leaf reduce to a central and two lateral groups, which are

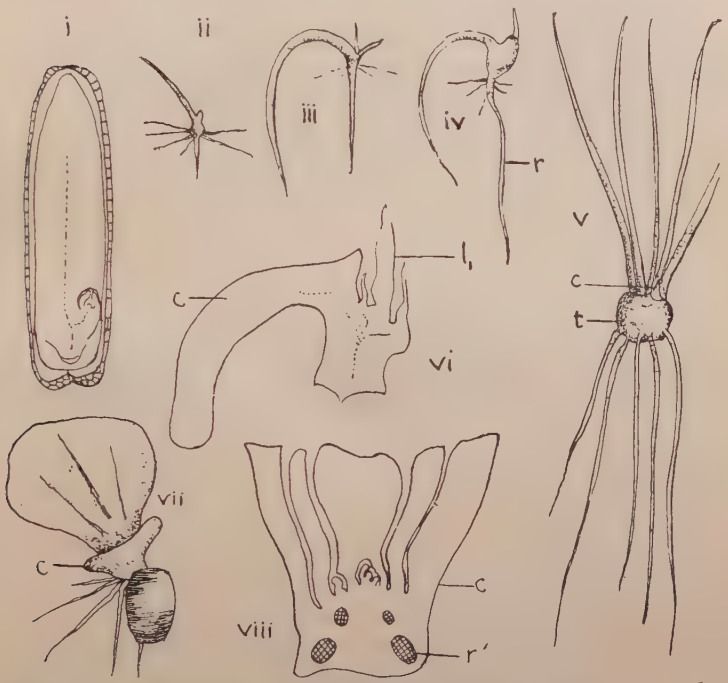

Fig 1.—i–vi. *Aponogeton abyssinicus*. i. Longitudinal section of ripe seed (×20). ii–iv. Seedlings three, six, and eight days old (×7). v. Seedling two months old, showing tuberosity: the remains of the cotyledon have persisted (×7). vi. Longitudinal section of seedling a few days old. vii–viii. *Pistia Stratiotes*. vii. Seedling a week old (×20). viii. Longitudinal section of seedling figured in vii.

c = cotyledon; *r* = primary root; *r'* = adventitious root; *t* = tuber.

joined by the cotyledon strand; a triarch arrangement results. At the root-hair region the root becomes diarch; lower, the xylem is reduced to a single element. Three or more patches of aerenchyma appear in the cortex.

(ii) *Four-weeks-old Seedling.*—At the upper limit of the tuber the bases of four leaves and the remains of the cotyledon sheath surround the plumular bud. The strands pass in close succession into a central solid axis. Adventitious

roots originate at this level. The swollen hypocotyl consists of large, starch-storing parenchyma, protected by two or

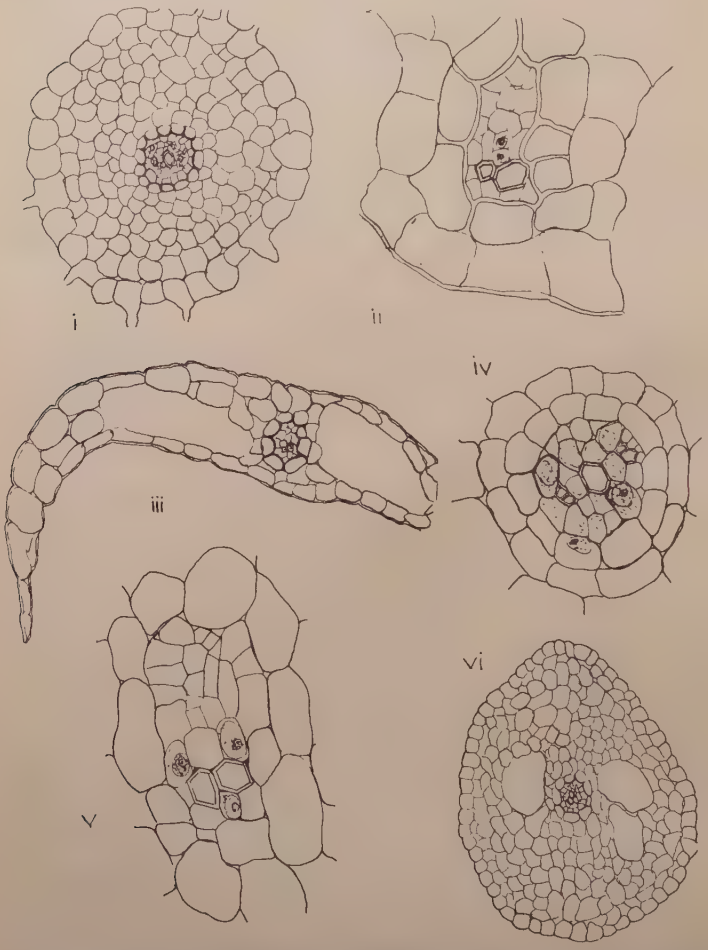

Fig. 2.—*Aponogeton abyssinicus*. i. Transverse section of primary root of seedling four weeks old (×200). ii. Transverse section of cotyledon strand in the sheath of same seedling (×400). iii. Transverse section of cotyledon sheath (×150). iv. Stele of primary root figured in (i) (×400). v. Transverse section of cotyledon strand in the lamina: seedling one week old (×500). vi. Transverse section of lamina of cotyledon showing air cavities: seedling one week old (×100).

three layers of suberised cells and traversed by strong vascular strands supplying five or six rootlets similar to the primary root. They have a simple stele, consisting of a central xylem

element enclosed by phloem and parenchyma, sheathed by an endodermis with thickened outer and radial walls. The cortical cells are large and thin-walled.

Aponogeton distachyon.

The embryo repeats the internal and external morphology of the species described, but at maturity is much larger (length 5–6 mm., maximum diameter 2 mm.).

Arber (2) refers to the food storage in the cotyledon of the embryo, and figures two stages in germination.

JUNCAGINACEAE—*Triglochin maritimum.*

Seeds were obtained from plants in Aberlady Salt Marsh but only two germinated. Seedlings were therefore collected from the Marsh in the following spring.

The seed has a convex and two plane faces and is 4 mm. long. The testa is pale yellow. The ripe seed is exalbuminous. Schlickum (127) describes the short, thick hypocotyl and weak radicle of the mature embryo. The second foliage leaf is differentiated before germination.

Very young seedlings are devoid of root hairs, which are produced in a ring from a swollen collar at the upper part of the short blunt radicle at the stage when the cotyledon becomes erect. Although the primary root is initially weak, it lengthens after the appearance of the first two leaves. The cotyledon, the most conspicuous organ of the young seedling, is at first cylindrical; later it has an open sheath and narrow lamina; there is little differentiation towards the suctorial tip. The slowly developing plumule appears through a slit towards the base of the cotyledon. Intravaginal squamules (T. G. Hill's "sessile glands" (71) and Schlickum's "adventitious buds") occur even in the axil of the cotyledon. The cotyledon gradually dies back, and the sheath becomes partially destroyed by the growth of adventitious roots through it.

Anatomy.—In the young seedling the cells of the suctorial tip of the cotyledon contain no starch, but the free part is rich in starch, oil, and aleurone. The epidermis, which has a thickened outer wall and consists of medium-sized cells, encloses a ground mass of five or six rows of parenchyma with

large intercellular spaces, the outer layers being chlorophyllous (fig. 4). The base of the cotyledon encircles the plumular

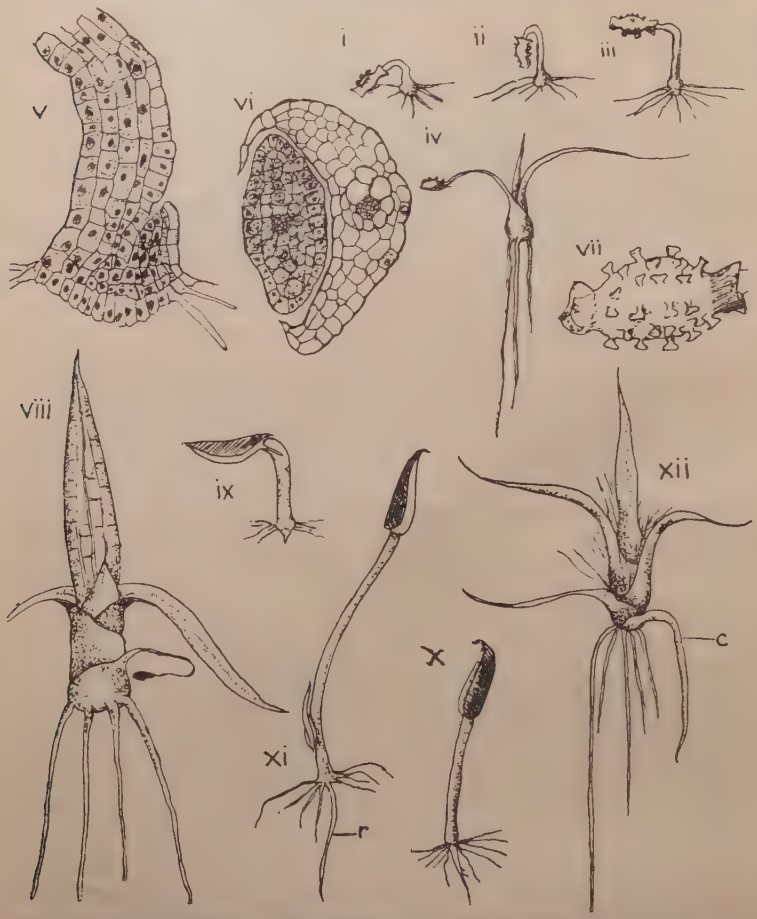

Fig. 3.—i–viii. *Philydrum lanuginosum*. i–iii. Seedlings two, four, and six days old (× 8). iv. Seedling ten days old (× 8). v. Longitudinal section of seedling a day old, showing the weak differentiation of the plumule (× 80). vi. Transverse section of cotyledon sheath and base of the first leaf in a seedling one week old (× 80). vii. Seed (× 25). viii. Seedling three or four weeks old: the lamina of the cotyledon has begun to shrivel (× 5). ix–xi. *Triglochin maritimum*: seedlings three, six, and ten days old (× 4). xii. *Eriocaulon* sp.: seedling three weeks old: the cotyledon assists in anchoring the plant (× 5).

c = cotyledon; r = primary root.

bud, the first leaf primordium, and a squamule. The upper epidermis of the sheath has larger and thicker outer walls than the lower epidermis. Stomata occur, though not found by

Schlickum. Lewin (95) discovered one or three strands proceeding through the cotyledon ; Schlickum pointed out that where three were found he had probably mistaken the first leaf for the cotyledon, the latter being already dead. In no instance in the present investigation had the cotyledon more than one strand. The simple collateral strand (fig. 4), which is surrounded by a sheath of small cells, proceeds centrally through the cotyledon, being diverted temporarily above the plumular mass. A hypocotyl is practically absent.

The primary root (fig. 4) has a wide cortex and a small diarch medullated stele, an observation of interest in view of van Tieghem's contention that the xylem strands in the adult root do not meet in the centre but are separated by parenchyma (a statement questioned (71) by Hill). The pericyclic cells are as large as those of the endodermis, which is thickened on the radial and outer walls. The hypodermal layer stains like the epidermis. The swollen collar (fig. 4) from which the rings of root hairs arise is produced not by additional layers but by the enlarged nature of the cells, which are roughly rectangular in outline and strongly meristematic. The radial symmetry of the cotyledon is repeated in the first leaf, the three strands of which run through the blade and unite at the tip. The second leaf is similar but has more photosynthetic tissue than the first. Succeeding leaves are of the same type. Their sheaths remain colourless and serve as storage organs for starch (127).

Eriocaulaceae—*Eriocaulon* sp.

The seed, originally from Assam, was obtained from Kew. The initial stages of germination were not observed.

The fruit is produced from a trilocular ovary containing one elliptical seed per locule. The seed is covered with a testa of two layers of cells, the inner coloured yellow or red-brown. The small, lentiform embryo lies opposite the hilum in starchy endosperm.

Germination is of the same type as for *Triglochin* and *Aponogeton*. Development is slow. After a few weeks a ring of numerous strong adventitious roots replace the primary root. Between the long, sharply pointed leaves, which are placed in close succession on a short, stout axis, there arise tufts of long unbranched multicellular hairs,

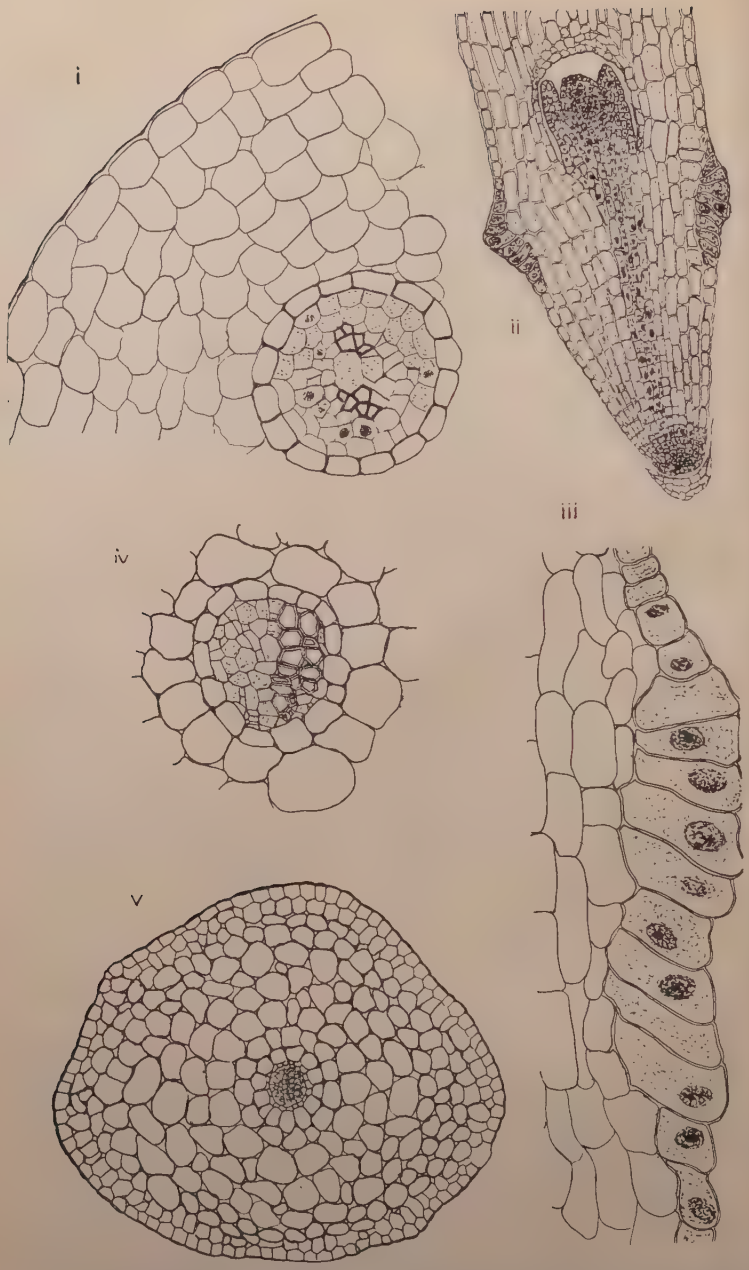

FIG. 4.—*Triglochin maritimum.* i. Transverse section of primary root (×500). ii. Longitudinal section of seedling a day old, showing the plumular bud, primary root, root cap, and enlarged epidermal cells from which the garland of root hairs is produced (×50). iii. Enlarged cells figured in ii (×200). iv. Transverse section of cotyledon strand towards the base of the lamina (×200). v. Transverse section of cotyledon towards the base of the lamina (×100).

originating apparently at the base of the leaf at its insertion on the axis (fig. 3).

The upper part of the linear cotyledon is almost cylindrical, but towards the base it becomes more flattened. A single

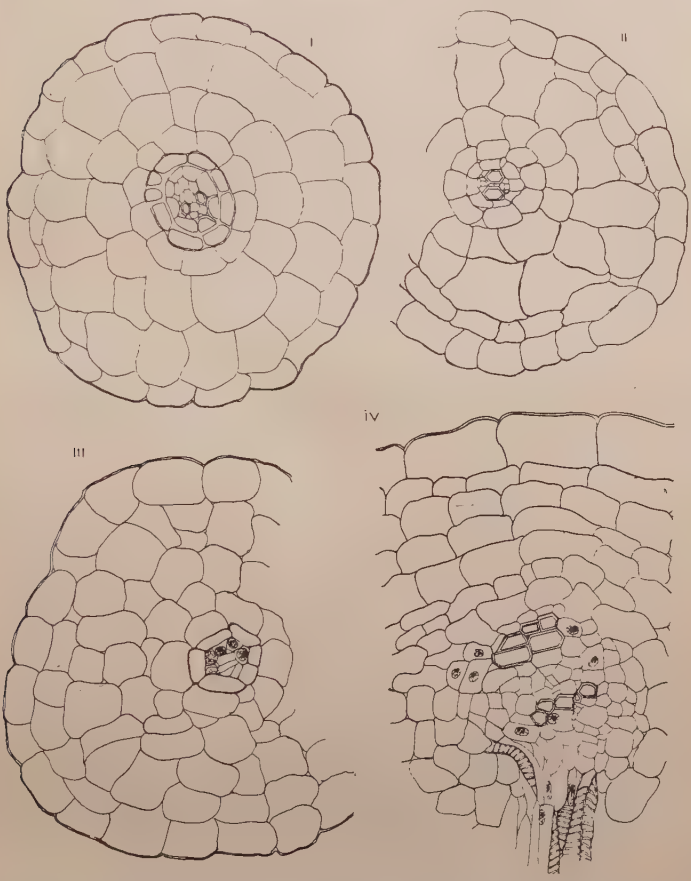

Fig. 5.—i. *Eriocaulon* sp.: transverse section of primary root (×500). ii. Transverse section of adventitious root, showing complete absence of suberisation in the endodermis (×500). iii. *Philydrum lanuginosum*: transverse section of primary root (×50). iv. *Eriocaulon* sp.: transverse section at the level at which the cotyledon strand becomes oblique and joins the plumular traces (×500).

vascular strand is enclosed by a remarkably strong sheath of seven to nine thickened cells, the larger towards the outer surface (fig. 6, i). This sheath is itself surrounded by a ring of very large, thin-walled cortical cells. Two large air cavities

occurring on each side of the vascular strand are bridged over by diaphragms of star-shaped chlorenchyma. The adaxial epidermis consists of one layer of cells, but the opposite surface

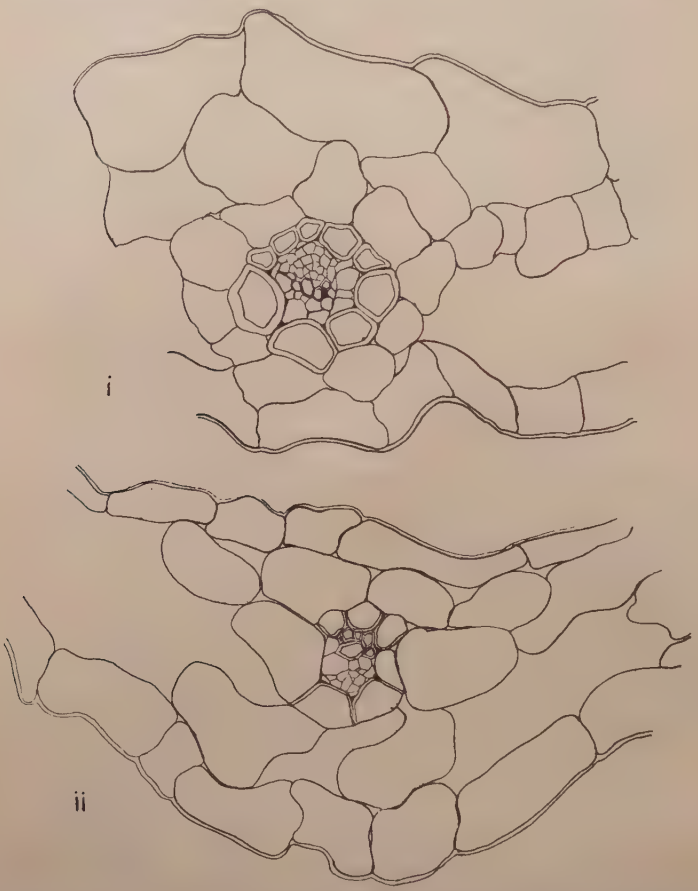

Fig. 6.—i. *Eriocaulon* sp.: transverse section of the base of the cotyledon, showing the pronouncedly thickened sheath (×500). ii. *Philydrum lanuginosum*: a similar section for comparison with that of *Eriocaulon* sp. (×500).

is made up of an epidermal layer of large parenchyma (rectangular in transverse section) and one hypodermal layer. Upper and lower epidermis are thinly cutinised. A close resemblance, externally and internally, exists between the cotyledon and first leaf. In the latter, which has in addition a pair of lateral traces, two large air spaces flank the mid-rib

which, like the cotyledon strand, has a simple stelar structure and a double sheath. The mature leaf of *E. septangulare* repeats these features. Ruhland (116) refers to the same internal fenestration in the early leaves of *E. Ulaei*, Ruhl., and in every respect there is a close similarity also to the leaves of *E. decangulare*, a plant of sphagnum swamps studied by Holm (77). He found each mestome bundle of the leaf enclosed by a sheath, which at first glance was considered identical with the parenchyma sheath seen in many genera of other orders, but it was missing in the stem, and in longitudinal section the cells were indistinguishable from a collenchyma sheath. Another sheath, with thicker walls, lies within the first. According to Poulsen (106) the outer represents true parenchyma, the inner one sclerenchyma. Such an opinion would apply to the sheaths of the cotyledonary strand of the species under investigation.

Transition.—The plumular traces in a young seedling reduce to five which form a central group of metaxylem with two protoxylem groups on one side and two phloem groups on the other. The cotyledonary strand passes towards the centre and joins them, forming a single bundle (fig. 5, iv). The root stele is diarch, consisting of a few elements of xylem and phloem surrounded by a pericycle of six or seven cells, thickened in some cases on all walls, in others only on the outer tangential wall, or on all but the inner tangential wall (fig. 5, i). The endodermis is composed of nine or ten larger cells thickly suberised on all but the outer tangential walls. The cortical cells are large and thin-walled, the thinly cutinised epidermal cells large and regular. These features are repeated by the young adventitious roots (fig. 5, ii), but the pericyclic cells, though large, are thin-walled, and the suberisation of the endodermis is almost imperceptible. The delicate cortex tends to break on sectioning. Most steles contain only two metaxylem elements, but later the adventitious roots become polyarch and aerenchymatous. Holm, who found wide lacunae in the root cortex of *E. decangulare* and the horizontally placed diaphragms at intervals, classes such roots as " simply nutritive, since they possess no pronounced power of resistance and are not contractile or especially adapted for storage." The epidermis of the short rhizome (1–2 inches long) in the adult is developed into long hairs.

Noteworthy points are the striking resemblance in the external and internal morphological features of the cotyledon and first foliage leaf, the parenchymatous and sclerenchymatous sheaths surrounding the cotyledonary strand, the unusual pericyclic development, and the constancy in different species of the peculiar anatomical features.

Philydraceae—*Philydrum lanuginosum.*

The ripe seed (0·5 mm. long) is spindle-shaped, non-endospermic, with peg-like outgrowths on the outer seed coat (fig. 3). The spiral bands on the testa, figured by Klebs, were not observed. The embryo is straight.

Germination (fig. 3) resembles that of *Triglochin*. The cotyledon consists of a very short base, linear lamina, and short tip. The primary root is short and blunt, protected by a flattened root cap. The plumular bud arises immediately above the primary root. Only the first leaf is differentiated at germination; it emerges by a lateral slit, and the cotyledon carrying the seed coat on its tip becomes erect. A ring of root hairs develops above the root cap. The primary root, which elongates below the short hypocotylar region, is for some time the principal root. When two or more foliage leaves are functioning, adventitious roots arise round the flattened base of the axis, which increases considerably in girth (diameter more than 1 mm.). The isobilateral equitant leaves arise in close succession.

Anatomy.—The tissues of the young cotyledon which has radial symmetry are similar to those of genera already described. Large cells, thinly cutinised, comprise the upper and lower epidermis, and the mesophyll is reduced to two layers of loose chlorenchymatous tissue. A single vascular strand (figs. 3, 6) proceeds from the cotyledon tip to the primary root, its course being vertical save where it deviates near the plumular bud. The stele is composed of four xylem elements and a little phloem enclosed by a sheath, resembling that of the cotyledon strand in *Eriocaulon* sp. Anatomically the primary root (fig. 5, iii) is exceedingly simple. An epidermis of large, regular cells encloses a cortex four or five layers deep. The small stele has a prominent endodermis of six or more large cells thickened on all but the inner tangential wall,

surrounding a group of four xylem elements and an equal bulk of phloem. The epidermal cells of the first leaf are large with clear contents; the mesophyll is two or three layers deep. In older seedlings long and wide lacunae develop between the mid-rib and the two lateral strands.

Longitudinal sections of the ripe embryo of *Pontederia cordata* (Pontederiaceae) reveal a structure similar to that of *Philydrum*. The embryo of *Pontederia* has apparently not been previously described.

Alismaceae.

Embryos and seedlings of *Sagittaria guyanensis* and *S. sagittifolia* were found to agree closely in structure with *Alisma Plantago* (also examined), which has been investigated by several morphologists (65, 87, 97, 127, 146, 149). The development of the primary root and ring of root hairs, morphology of the cotyledon and young leaves are almost identical with those of the genera already described.

Naiadaceae.

Observations on the macropodous embryo of *Zostera marina* confirm those of previous investigators (150). Further description is accordingly unnecessary. Klinsmann (88) and Irmisch (83) describe the seedling of *Najas major*, which closely resembles the *Alisma* type.

Juncaceae.

The germination and seedling morphology of the species of *Juncus* examined (*J. effusus*, *J. niveus*, *J. arcticus*, *J. Gerardi*) agree with those described by Laurent (92). The seed is extremely small. Germination is epigeal. Simplicity in the seedling structure characterises the genus, the cotyledon having a single collateral strand, and the first leaf, which resembles the cotyledon, a mid-rib and a pair of lateral strands.

Laurent found the internal structure of the seedlings of *Luzula* identical with that in *Juncus*, and recorded triarchy in the primary root. Evans (45) followed the development of the seedlings of three species of *Luzula* (making

observations in particular on the growth of the hypocotyl). The only species examined by the writer are *L. campestris* (which has been described by both authors) and a species given as *L. sylvestris*.

Aroideae—*Pistia Stratiotes* (fig. 1, vii–viii).

Longitudinal sections were made of the young seedling, but lack of material prevented a more thorough investigation. The suppression of the primary root, early origin of numerous adventitious roots, and short thick axis are obvious from the sections. The cotyledon, which is aerenchymatous, acts as a float from the time of germination. According to Sargant (122) the suppression of the axis in the embryo of the plant is an adaptation to its surroundings, since a stem is a feature of the mature plant. Hegelmaier (66) and Koch (89) figure the ripe embryo, and Velenovsky (150) the stages of germination.

Additional Genera described in Literature.

Velenovsky (150) figures the embryo of certain genera of Potomogetonaceae (*Ruppia*, *Zannichellia*, *Posidonia*) and the embryo and seedling of *Typha*. Irmisch (83) and Klinsmann (88) describe the seedling of *Stratiotes aloides*, which resembles *Najas*. Lubbock (97) gives an account of two unusual marine types, *Thalassia* and *Halophila*, the latter investigated in detail by Bayley Balfour (5). The cotyledon of *Halophila* has a single vascular strand, and the first leaf a mid-rib and a pair of lateral traces. In the embryo the hypocotyl is enormously developed, but the primary root and true foliage leaves are suppressed. Campbell (20), who examined the embryo of a series including *Sparganium*, *Najas*, and *Zannichellia*, noted that the mature embryo of the three have in common a highly differentiated plumule, a dominance of cotyledon, and poverty of primary root.

Summary.

Arber (1) notes that the germination and development of the seedling in aquatics vary according to the natural affinities of the plants in question, and are characterised by few peculiarities related to the environment, except a very

frequent reduction of the primary root. She mentions the reduced primary root, the anchorage where necessary by root hairs, and in the Helobieae the absence of endosperm, and the macropodous embryo—more than a few peculiarities. The external morphology alone diverges from that of a normal geophytic seedling. The comparative study of the seedlings reveals a remarkable uniformity of development and structure which may be briefly summarised :

(*a*) The type of germination and rate of development are common to all. There is a similarity between the cotyledon and first leaf in general morphological features, and a characteristic simplicity of shape and structure.

(*b*) At germination the primary root is weak but grows considerably at a later stage. A garland of strong root hairs is produced immediately after germination at the upper limit of the primary root, and adventitious roots soon make their appearance.

(*c*) The embryo stores food in a greatly swollen hypocotyl or in the cotyledon. Frequently aerenchymatous tissue occurs in the ripe embryo.

(*d*) The close succession of leaves arising on a short axis give the plantlet a squat appearance.

(*e*) The anatomy is uniform even in details such as the sheathed cotyledon strand and the distribution of aerenchyma. The structural reduction characterising the adult is reflected in the simple internal economy of the seedling.

Epiphytes.

Bromeliaceae.

Owing doubtless to the difficulties involved, there are few publications on the germination of epiphytes. Schimper (126) first suggested that, although reproductive organs and processes were not influenced by the plant's peculiar mode of life, germination might be exceptional, a hint which bore fruit in the work of F. Müller, who made observations in 1895 on seeds and seedlings mostly of the subfamily Tillandsieae. Nine years later Billings described the germination of *Tillandsia usneoides*, which usually propagates itself vegetatively, but ignored Müller's findings on the genus. In 1922 Szidat published a review of the seeds of Bromeliaceae and their

adaptations to an epiphytic life, and described the germination for each grouping made. It is regrettable that, except for a careful study by Gatin (56), publications give little or no account of the internal structure of embryo and seedling. More recently Thomas and Holmes (144) have made a thorough research on the germination and seedling of *Ananas sativus*.

The Bromeliaceae have been classified with the vegetative characters and mode of life of the plant as a basis. Taking into account the nature of the appendages of the leaf epidermis (stellate hairs, etc.) and mode of nutrition, Tietze (148) divides the family into (*a*) terrestrial forms of low habit, having no special mechanism for conserving or obtaining water, but with an efficient root system, *e.g. Puya* and *Dyckia* ; (*b*) terrestrial forms where highly specialised scales absorb water, *e.g. Ananas* and some Pitcairnieae ; (*c*) low-growing epiphytes having great leaves in a rosette, in which water absorption is augmented by epidermal scales in order to compensate for a weak root system. Keiline (86), making the habit and leaf structure his basis, obtained three similar groups. Szidat (139) claims that the seed is absolutely diagnostic, and gives the following classification:—

I. Bromelieae—Facultative Epiphytes.—Testa without appendages. Seed pear-shaped. Embryo small. Endosperm copious.

II. Pitcairnieae—Terrestrial.—Seed dispersed by wind. Seed torpedo-shaped.

III. Tillandsieae—Obligate Epiphytes.—Outer layer of testa hairy.

Germination of Types Representative of Szidat's Groups.

I. *Facultative Epiphytes—Bromelieae.*

Billbergia zebrina.

Müller figures five stages in the germination.

The seed (about 4 mm. in length) is roughly pyramidal. The dark brown testa consists of two layers ; the inner walls of the principal layer are unusually thickened. The copious endosperm is starchy, with an outer aleurone layer. The embryo (fig. 67, 6*a*) is almost as long as the seed, tapering at the suctorial tip of the cotyledon, widening considerably

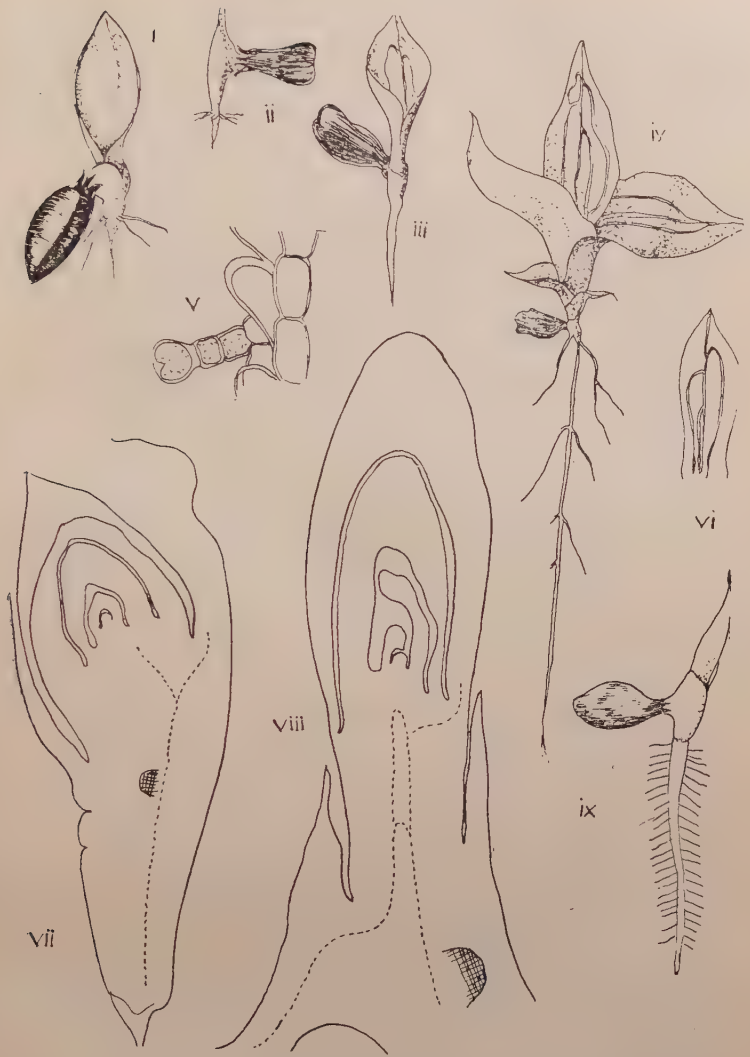

FIG. 7.—i. *Aechmea glomerata*: seedling a few days old (×5). ii–viii. *Billbergia zebrina*. ii–iv. Seedlings three days, five weeks, and three months old (×3). v. Glandular hair and papillose cells on the epidermis of the first leaf. vi. Venation of the first leaf (×3). vii. Longitudinal section through young seedling before development of the ligule has occurred; the dominance of the plumular bud is noteworthy. viii. Longitudinal section through a seedling in which the young leaves have ruptured the ligule; the passage of the cotyledon strand in the lengthy first node is indicated. ix. Seedling of *Acanthostachys strobilaceae* (after Klebs).

towards the basal end. The well-developed plumular bud is lateral, its vascular meristem almost parallel to the cotyledonary trace, but the primary root lies at an obtuse angle to both. The vascular skeleton is accordingly asymmetrical.

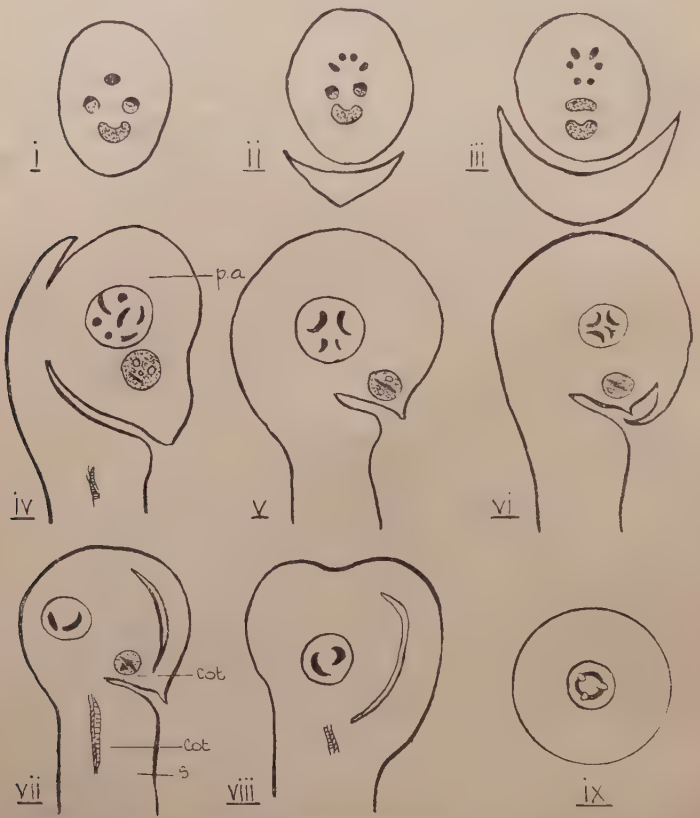

Fig. 8.—*Billbergia zebrina*. Transverse sections from the first internode (i) to the upper limit of the primary root; (viii) shows the cotyledon strand passing from the cotyledon sucker into the cortical zone at the base of the first internode.

cot = cotyledon strand; *p.a* = plumular axis; *s* = sucker.

Germination.—No definite mechanism is apparent for the rupture of the seed coat. The radicle breaks through the testa at the apex of the seed, a ragged fringe of six to eight teeth being left, as a result of the nature of the thickening of the cell walls. A ring of root hairs arises at the upper extremity of the radicle, the blunt tip of which is protected

by a massive root cap (fig. 7). The primary root and plumule, after their withdrawal from the seed, appear more in alignment with each other (fig. 67, 6*b* ; fig. 7, vii), but the sucker of the cotyledon remains at an obtuse angle to the remainder of the embryo for a few days, after which the organs of the

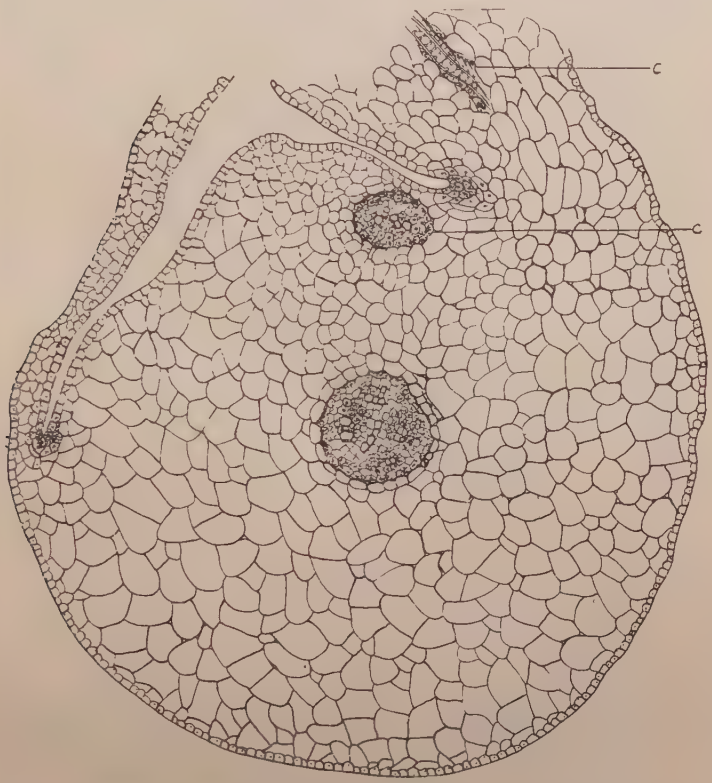

Fig. 9.—*Billbergia zebrina*. Transverse section through the base of the first internode and part of the cotyledon sucker, showing the passage of the cotyledon strand (*c*) into the internode. The course of the strand is bent (see fig. 7, viii), hence it appears twice in transverse section (× 100).

seedling attain their final orientation ; the axis of plumule and radicle then becomes vertical and at right angles to the sucker (fig. 7, viii). The primary root in a week-old seedling is approximately 8 mm. in length, the total length of the seedling being 12 mm. The cotyledon at this stage consists of an extremely short, blunt suctorial tip (less than 0·5 mm.), a sheathing base (1–1·5 mm. long), tapering downwards to

the primary root, and the ligule, the most highly developed part of the cotyledon. The first leaf which, on elongating, escapes by an apical slit in the ligule is the same shape as succeeding foliage leaves, but never attains the size of the second leaf, which in its turn is smaller than the third. Its maximum breadth and length are equal, and it is anatomically

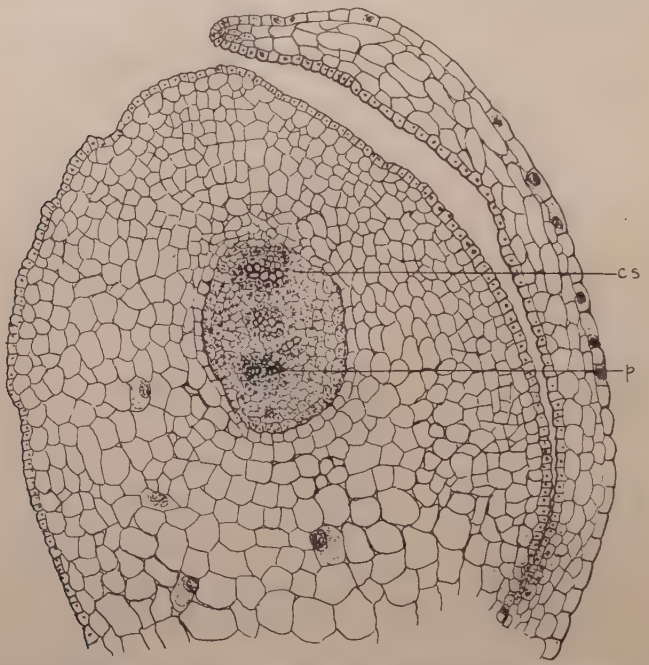

FIG. 10.—*Billbergia zebrina.* Transverse section of the first internode and part of the cotyledon ligule at the level at which the cotyledon trace is incorporated into the central stele (× 100).

c.s = cotyledon trace; *p* = traces of the central stele.

simple, having a mid-rib and two lateral strands. The rosette habit of the adult plant is indicated by the time that four or five leaves are expanded (fig. 7, iv).

Anatomy. Two-days-old Seedling.—The widest diameter of the plant is at the level of the plumular bud. The single cotyledonary strand proceeding downwards from the suctorial tip is diverted from its central position by the plumular mass. At the base of the short plumular axis part of the cotyledon strand moves inwards, and branches to supply the plumular meristem. A stele with scattered elements persists to the

transition which occurs at the upper limit of the root-hair region. The root stele is triarch.

Six-days-old Seedling.—Passing from the suctorial tip the cotyledon strand pursues an upward oblique course and enters the plumular axis at the base of the ligule and continues an almost vertical course up the internode (figs. 8, 9); two branches from the cotyledon trace supply the first leaf and plumular meristem. The main cotyledon trace then bends and proceeds downwards. Its descending trace forms part of the axillary stele, which consists of approximately double the number of xylem and phloem groups comprising the original cotyledon trace (see fig. 10 and central trace in fig. 9). It may be regarded as composed of both cotyledon and plumular vascular elements (an observation confirmed by a comparison with the axillary stele of the younger seedling). The xylem reduces from seven or eight groups to four, then two crescents. Further rearrangement gives a medullated triarch root stele, which lower becomes diarch.

Billbergia Breauteana was also examined. It differed in no essential from *B. zebrina*. Gatin has described the anatomy of the embryo and the external morphology of the very young seedling of *B. violaceae* (56).

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Seedlings of this plant showed obvious affinities with *Billbergia* in the type of endosperm, testa, germination, cotyledon, and primary root. The seed was obtained from British Honduras, and up to the present has not been named. Absorption of endosperm is slow, and the seed remains attached to the small suctorial tip for several weeks. Adventitious roots aid the primary root which produces lateral roots. The first leaf is delicate in texture; in venation it resembles that of *Billbergia*, and is provided with marginal ocelli and glandular hairs.

Anatomy.—There is a single cotyledon strand. The stele of the first node is enclosed in a strong sheath and consists of two well-developed strands with the protoxylem patches almost touching, after the fashion of a double bundle. The hypocotylar stele also is characterised by a powerful sheath, consisting of a double layer of large, strongly thickened cells

and surrounding five patches of xylem (a little phloem being associated with each) separated by rays of a single layer of parenchyma. The root, which has an exceptionally strong endodermis, is triarch in a young, pentarch in an older, seedling.

Aechmea glomerata.

The emergence and appearance of the radicle and circle of root hairs in the first week recall the germination of *Billbergia* (fig. 7, i). Szidat (139) notes that in *A. tinctoria* the mechanical strength of the primary root is not entirely responsible for the rupture of the testa, since the root produces a secretion which partially dissolves the cells of the testa in the neighbourhood of the growing-point. He also comments on the presence of a root cap, the hypocotyl and the green cotyledonary sheath, which is pierced by the first leaf on the ninth day, and considers the exceptional arrangement of root hairs to be advantageous in securing the epiphyte on the branches of trees. The poor development of the primary root, early appearance of adventitious roots, long functioning of the suctorial tip of the cotyledon, and adequate endosperm might also be connected with the habit. Gatin (56) has described the similar embryo and germination of *A. miniata*.

Observations on the germination of *A. glomerata* reveal the same features. The pronounced ligular development, seen in *Billbergia*, is absent, though the arching upwards of the margins of the cotyledon sheath affords protection to the plumule.

Anatomy of Seedling Five Days Old.—A single collateral strand (fig. 11, iv) extends from the well-developed stopper-like tip of the cotyledon to the sheath. The plumular bud is immediately above the base of the cotyledon. On the side remote from the seed the sheath is slit almost to the base, but the overlapping margins give protection to the young leaves. The ground tissue of the cotyledon is parenchymatous. Sunk stomata occur. The first and second leaves have a mid-rib and a pair of lateral strands. The lengthy hypocotyl is traversed by a collateral strand, sheathed by the remarkable endodermal sheath found in other genera of Bromeliaceae. The stele of the primary root, which has an exceedingly small diameter, is triarch. In seedlings a fortnight old the

seed tends to be lifted above the surface, possibly the result of the continued growth of the hypocotyl.

Seedlings of other genera in this group were not examined in the present investigation, but previous accounts of three genera may be referred to.

Klebs classes *Acanthostachys strobilaceae* with Type I. (p. 179), and comments on the exceptionally thick covering of long root hairs (fig. 7, ix). The germination is evidently similar to that of *Billbergia*. Szidat, recognising the presence of a ligule without so designating it, describes the seedling as having a club-shaped sucker, derived not from the tip but "from the back of the cotyledon." The ligular development is apparently more pronounced than in *Billbergia*. Gatin (56) gives an account of the embryo and seedling of *Karatas amazonica*, the anatomy of the embryo and germination of which belong to the *Aechmea* type.

An investigation of the early life and structure of *Ananas sativus*, made by Thomas and Holmes (144), reveals that the seed is longer than that of *Billbergia*, has a leathery ridged testa, three layers thick, with tufts of hairs on the ridges. An outer aleurone layer and a mass of starch-containing cells comprise the endosperm. Seven stages are given of the hypogeal germination. Emergence of the primary root is due to expansion and elongation of cotyledonary cells. Ontogenetic development is slow. After three weeks the cotyledon is a cylindrical plug, in the hollow of which the plumule develops, the wall being thin on one side for its emergence; a short cotyledon sheath is produced. A single collateral strand runs through the entire length of the cotyledon and contributes with a less differentiated plumular strand to the hypocotylar stele. The independent adult form is established after three months, when the endosperm is finished and the primary root replaced by adventitious roots. The hypoderm on the upper surface of the plumular leaves stores water. Epicotylar and hypocotylar axes are short. The young root is apparently diarch, but later may be triarch or tetrarch. A distinct stelar structure consisting of a pericycle of several cell layers is found at the level of insertion of the second leaf.

II. *Terrestrial—Pitcairnieae.*

Dyckia.

Dyckia floribunda.—A membraneous outer integument, which provides a wing for the flat seed (fig. 11), soon rots. The endosperm is an ovoid mass 3 mm. long. The embryo, which consists mainly of cotyledon, is well differentiated in the ripe seed, and occupies a lateral position. The blunt radicle lies opposite the narrow end of the seed. The first leaf rudiments are clearly differentiated from the cotyledon tissue, a deep cotyledon slit occurring above the plumular bud.

Germination (fig. 11).—A seedling two days old is 4–5 mm. long. The primary root (0·5 mm. in length) is covered with long root hairs, very tenacious of soil particles. The hypocotyl (1·5 mm. long) is smooth and transparent. The cotyledon broadens from the base upwards, the seed being attached to the extremity, which is bent at right angles to the axis. Within six weeks or so a lateral rupture results in the gradual unfolding of the cotyledon and expansion of its wide green blade, the advantages of an entirely sheathing and a photosynthetic cotyledon being thereby obtained. Contrasting with the advanced differentiation of the young plant is the slow development subsequent to germination.

A six-weeks-old seedling is approximately 6 mm. in height. Its appearance of bulk is produced by the cotyledon, which now consists of a blunt suctorial tip, occupying not more than one-third of the seed, and a long, wide lamina, tapering upwards into the tip, downwards into a comparatively short sheath. The root, which is densely covered by root hairs, is still a small fraction of the total length of the seedling.

Eleven-weeks-old Seedling.—There is now a marked difference in the symmetry of the plant, which has assumed the rosette habit. The first leaf is opposite and equal in size to the cotyledon, to the tip of which the remains of the seed still adhere. The primary root, 7 mm. long, exceeds the aerial portion of the plant in length, and is reinforced by a buttressing adventitious root. The first and succeeding leaves possess marginal teeth.

Four-months-old Seedling.—Few new features have appeared. The fourth leaf appears in the rosette between the position of the second and third leaf. The tendency for a

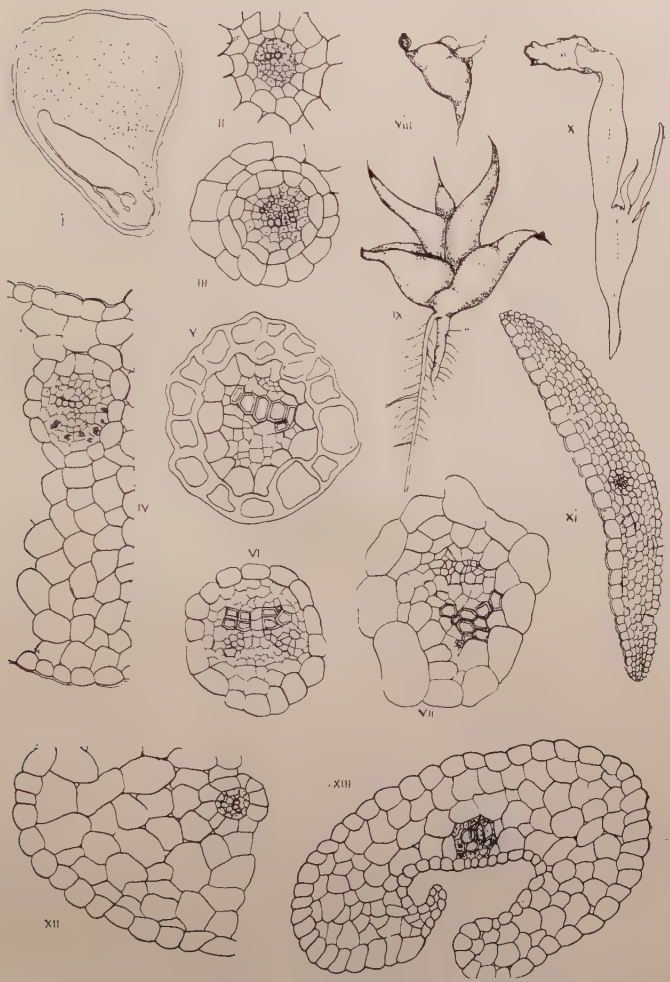

Fig. 11.—i. *Dyckia floribunda*: longitudinal section through ripe seed (×10). ii–iv. *Aechmea glomerata*. ii. Transverse section of primary root (×250). iii. Transverse section of hypocotyl (×250). iv. Transverse section of cotyledon towards the base (×500). v–vi. *Dyckia floribunda*. v. Transverse section of primary root (×500). vi. Transverse section of cotyledon strand (×500). vii. Transverse section of cotyledon strand of *Dyckia remotifolia*. viii–x. *Dyckia floribunda*. viii. Seedling six weeks old (×2). ix. Seedling four months old (×5). x. Longitudinal section of seedling figured in viii. xi. Transverse section of cotyledon lamina of *Puya caerulea* (×50). xii–xiii. *Pitcairnia xanthocalyx*. xii. Transverse section of primary root (×50). xiii. Transverse section of cotyledon (×50).

rosette habit is now marked. The primary root has not increased to any extent in length; lateral rootlets arise from the single cauline root, which is double the length of the radicle.

Seven-months-old Seedling.—Of seven seedlings of this age, each possessed only one cauline root 15–22 mm. long, and a primary root entirely covered with root hairs and of the same length as the plant at eleven weeks old. The cotyledon had shrivelled, and the fifth leaf was in an advanced stage of development.

Anatomy of a Week-old Seedling.—The single cotyledon strand (fig. 11) proceeds from the tip to the base of the sheath, acting as a mid-rib to the succulent, leafy body. The simple collateral stele is enclosed by a sheath. The mesophyll of the blade resembles the hypocotylar cortex. The first foliage leaf is supplied with a mid-rib and two lateral strands. Proceeding upwards, the procambial strand of the second and succeeding leaves dies out, consequently the cotyledon strand fuses only with traces from the first leaf. A little below the plumular bud it incorporates half of each lateral strand, and a sheath surrounds the strands from the first leaf and the cotyledon strand. Lower, the mid-rib divides, the halves lying on the arms of a right angle about the independent residue of the lateral traces. Further rearrangement gives a stele showing dipolarity, one-half contributed solely by the first leaf, the other by the latter and cotyledon. Below the hypocotyl the stele is diarch. The endodermis of the primary root (fig. 11) is composed of large, greatly thickened cells; at intervals it is apparently a double layer. The pericycle consists of one row of very large cells. Raphides were observed in the outer layers of the wide, water-storing cortex and in the hypodermal layers and mesophyll of the leaves. Glandular hairs occurred on the margin not only of the first leaf but of the cotyledon.

In seedling structure *Dyckia remotifolia* (fig. 12) resembles *D. floribunda*. The cotyledon strand remains independent for some length after the plumular strands coalesce. Triarchy is indicated in the hypocotyl, but the radicle is diarch. The development of pericycle and endodermis is again noteworthy. Longitudinal sections of seedlings of *D. brevifolia* and *D. rariflora* indicate their structure to be essentially similar to that

of the species described. At the end of the tenth month the seedlings had six leaves, the aerial part of the plant being 13–15 mm. in height.

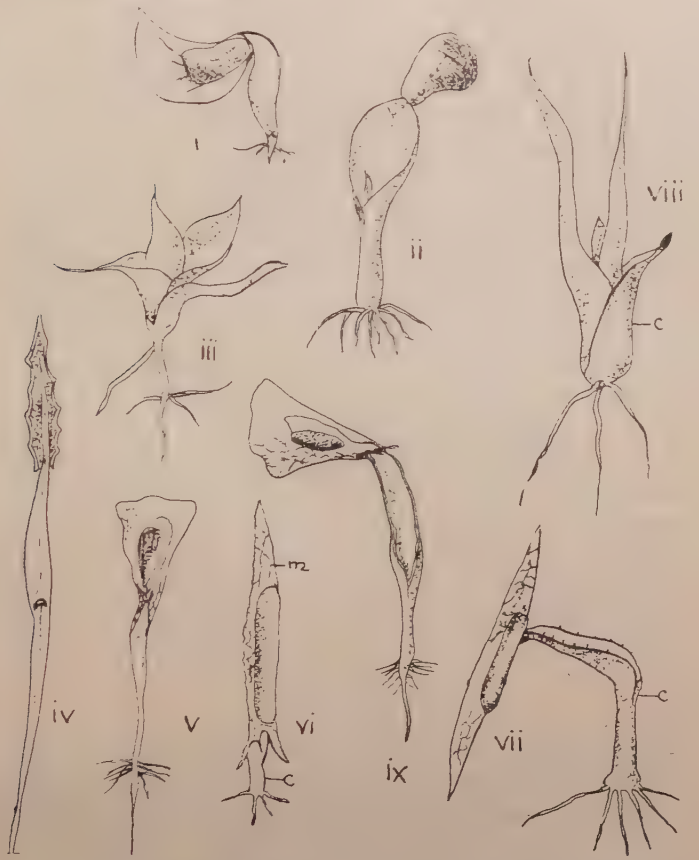

Fig. 12.—i–iii. *Dyckia remotifolia.* i. Seedling one week old (×5). ii. Seedling six weeks old (×5). iii. Seedling four months old (×4). iv–v. *Puya coarctata.* iv. Seedling two days old in longitudinal section (×10). v. Seedling sectioned and figured in iv (×5). vi–vii. *Pitcairnia xanthocalyx*: two stages in germination (×10). viii. *Dyckia remotifolia*: seedling four months old (×5). ix. *Puya caerulea*: seedling in which the lamina of the cotyledon is expanding (×10).

m = membraneous testa; *c* = cotyledon sheath.

Puya.

Puya caerulea.—The seed, embryo, and germination are similar to those of *Dyckia* (fig. 12). The seedling is characterised by a delicate, simple structure. The cotyledon tip

fills most of seed, endosperm being scanty. A fairly wide photosynthetic lamina, traversed by a single, rib-like cotyledonary strand, terminates in a short basal sheath which surrounds the poorly differentiated plumular bud. The first foliage leaf which has a mid-rib and two lateral strands slowly develops. In the early stages the greater length of the seedling consists of a slender, cylindrical hypocotyl which persists as a distinct region for at least one year. In the first week the primary root is less than 1 mm. in length.

Anatomy.—In the lamina of the cotyledon the vascular strand is embedded in a chlorophyllous layer (fig. 12). The upper epidermis, composed of large cells squarish in transverse section, stores water, while the lower epidermis consists of smaller cells. Simple glandular hairs occur on the epidermis. The three strands of the first leaf lie in a band of chlorophyllous tissue ; the upper epidermis, like that of the cotyledon, stores water. Spines occur on the leaf margin. The traces from the plumular bud and first foliage leaf reduce to two strands, with one of which the cotyledon strand unites. Hence half of diarch root stele supplies the plumule. The endodermis, as in *Dyckia*, is exceedingly strong.

Puya coarctata has a triarch root stele, but is otherwise similar in external and internal morphology to *P. caerulea.*

Pitcairnia.

The terrestrial mode of life, according to Szidat (139), is indicated in the seeds of the genus *Pitcairnia* by their specialisation for wind dispersal ; they are exceedingly light in weight and have a membraneous testa. Germination of *P. xanthocalyx* and *P. Andreana* was followed (the former previously described by Szidat). The small, delicate seedling resembles *Dyckia* in germination. A ring of root hairs is produced at the upper limit of the primary root and the tip of the delicate cotyledonary blade remains embedded in the scanty endosperm. From Szidat's account it would appear that the seed does not appear above ground. Actually the seed may be lifted above the soil by rapid elongation of the hypocotyl before the first leaf develops. The testa drops off the tip of the cotyledon at an early stage (fig. 12).

Anatomy.—The internal structure is almost identical with

that of *Puya* and *Dyckia*, but on a much-reduced scale. The seedlings examined were a few days old. The single collateral strand of the cotyledon acts as a mid-rib. Four chlorenchymatous layers lie between the upper and lower epidermis, which consist of small regular cells (fig. 11). Glandular hairs arise on the margin of the cotyledon blade. The plumule, at the stage of development examined, made no contribution to the root stele. The hypocotyl is cylindrical. A central collateral strand enclosed in a sheath of seven or eight very large, thin-walled cells passes into the root stele, in which three or four xylem elements are associated with a little phloem and confined by a strong endodermis.

Gatin mentioned the epigeal germination of *Pitcairnia spathacea* under the name of *Puya spatacea*, but gave little further information.

III. *Obligate Epiphytes—Tillandsieae.*

The seed is long, thin, and spindle-shaped, the embyro occupies more than one-third of the seed, and the testa is the most specialised in the entire family, its outermost layer having developed long, silky, multicellular hairs. Szidat divides the subfamily into two groups: (*a*) that including *Vriesea*, *Tillandsia*, *Guzmania*, and *Sodiroa*; (*b*) *Catopsis*.

(a) (i) *Vriesia Type.*

Vriesia vitellina.—Germination was observed by Müller. The embryo is large, cylindrical, and symmetrical. Excepting the plumule, the organs are little differentiated. The basal end of the testa holds the primary root cap-fashion. On germination elongation of the sheathing base of the cotyledon separates the cap-like basal end from the remaining testa; the "root cap" being loosely attached soon drops off. No primary root develops.

(ii) *Tillandsia Type.*

Müller (103) discusses the germination for a few species.

Tillandsia Gardneri.—The embryo occupies half the seed which, three or four days after sowing, swells and becomes green. The seed coat, too narrow to accommodate the bulky

structure within, loosens but does not crack, remaining intact until it is thrown off by the first foliage leaf. The latter, like the leaf of the adult, is equipped with a little lodicule.

Tillandsia usneoides.—Billings (12) describes the germination as normal : it occurred on the dehiscence of the capsule. Roots are completely absent in the seedling and adult plant. The cotyledon sheath appears double, due to bifurcation. The leaf first attains considerable size before stem differentiation begins, although in the adult plant the leaf is still small when the stem apex becomes distinguishable at its base. The first leaf has three vascular strands, each with a sclerenchymatous sheath. Water-storage cells are placed between chlorenchyma.

Tillandsia vestita.—Gatin (56) describes a germination similar to that of *T. Gardneri*. The morphology of the cotyledon recalls *Aechmea*, but the primary root aborts, and no adventitious roots are produced. At germination the suspensor atrophies owing to the degeneration of its cells. The cotyledon has a single vascular strand. The writer has examined preparations of *T. regina*, which repeats the features of *T. vestita*.

(b) *Catopsis Type.*

The remarkable tuft of long, silky hairs placed at one end of the seed is a diagnostic feature. They are hooked, a feature that Szidat correlates with the habit of the plant, which grows on the branches of trees of the primeval forest, the rough twigs affording an anchorage for the sharp hooks of the hairs. Germination resembles that of *Vriesia* : the primary root aborts.

Summary.

In this highly specialised family some degree of correlation exists between the type of germination and Szidat's grouping into tribes : the latter, it may be repeated, although primarily based on seed characters, is incidentally a grouping according to habit. Epigeal germination is characteristic of the Pitcairnieae, but the cotyledon of *Pitcairnia*, although a foliaceous photosynthetic organ, does not in the early stages lift the seed above the ground ; *Pitcairnia* would therefore seem to be a

transitional type. Germination in the Bromelieae is hypogeal, but the ligulate development of the cotyledon of *Billbergia* and *Acanthostachys strobilaceae* is merely suggested by the slight upward arching of the tissue around the cotyledon slit in *Aechmea* and the species of *Karatas* examined by Gatin (56). The term epigeal might be applied to the germination of the Tillandsieae, since the greater part of the seed is carried up on the enlarging cotyledon, the exposed part of which becomes green.

The shape and size of the suctorial tip of the cotyledon differs. It remains short and thick in the Pitcairnieae, but in the Bromelieae is a long-functioning, blunt, stopper-like organ. No distinct suctorial organ is differentiated in the Tillandsieae.

There exists a uniformity in the nature of the endosperm, but not in the proportion present in the seed. In spite of the appearance of bulk given by the testa, the seeds of the Pitcairnieae are amongst the smallest (0·3–1 mm. in length), and the embryo occupies more than half the seed. The Tillandsieae have long but narrow seeds (7 mm. for *Vriesia*), the embryo occupying one-third to one-half of the available space. The seeds of the Bromelieae are much larger and heavier, and, since in each the embryo is small, there is a preponderance of endosperm. The size of embryo is not directly related to the epiphytic life, but the weight of endosperm seems to show some correlation with the type of germination. It has been suggested that the large food reserve in the seed of the Bromelieae is a factor favouring their habit (139).

The development of the primary root is variable. At one end of the scale, terrestrial types (in which deep rooting is of primary importance) have from the first a persistent vigorous tap root. At the other are the obligate epiphytes, whose primary root aborts. Intermediate are the facultative epiphytes (rock and sand plants), having initially a short primary root, which later elongates and persists for three or four months. The more the primary root is restricted in its development, the better is the root tip protected. In the terrestrial forms the tip is protected in the normal fashion; a still more effective device is given by the basal end of the testa and suspensor in the Tillandsieae. The production of root hairs is variable. The ring of root hairs in the Bromeliea e,

probably compensating for the shortness of the primary root, acts possibly for fixation, since the seeds are not provided with long, entangling hairs, hooks, or gummy substance for their attachment before germination. The Pitcairnieae, in which the need for an efficient root system is obvious, show a marked development of root hairs.

The development of the plumule varies to some extent with the type of germination. Its lack of differentiation in the embryo and seedlings of epiphytes has been mentioned. The seedlings of the Pitcairnieae, which may be three or four weeks old before the first leaf is discernible, have no pressing need of an early foliage leaf. That the same period elapses in *Tillandsia*, in which the cotyledon is not foliaceous, may be referred to its extreme epiphytism. The first leaf of *Billbergia* and *Aechmea* makes its appearance a few days after germination, but *Ananas* of the same group is exceptionally slow in its production of leaves.

Development of the hypocotyl occurs only in the terrestrial forms.

The anatomical simplicity of Bromeliaceous seedlings and the constancy of certain features, such as the nature of cotyledon strand and root endodermis, may be due to extreme reduction as a result of the epiphytic habit, the final stage being seen in *Tillandsia usneoides*, in which degeneration of the vascular strands occurs.

The striking adaptation of the seed coat to assist dissemination, and, in epiphytes, fixation of the seed, has been fully discussed by Szidat. Odd points of interest arise, such as the double sheath of the cotyledon of *Tillandsia usneoides* (recorded by Billings), the liberation of an enzyme to assist in rupturing the seed coat of *Aechmea*, the occurrence in several genera of glandular hairs even on the cotyledon, and the striking similarity in the sheath of cotyledon strand and pericycle of certain species and *Eriocaulon* and *Philydrum*—genera phylogenetically related. The somewhat unusual course pursued by the cotyledonary strand of *Billbergia* merits further discussion. It would be interesting to determine whether the cotyledonary strand of the ligulate *Acanthostachys* behaves in a similar fashion.

Plants with Perennating Organs.

A.—Bulbous Plants.

LILIACEAE.

Tribe ASPHODELEAE—*Bowiea volubilis*.

The seedling is described by Lubbock (97).

Germination is epigeal (fig. 13). The cotyledon, the tissues of which show little differentiation, is for a year the only photosynthetic organ. During the first month it elongates rapidly. It is almost cylindrical, tapering from the base upwards. The tip, which bears the seed, later withers and casts off the empty testa. The poorly differentiated plumule is completely sunk in tissue and placed in a median position at the base of the cotyledon, lateral to the cotyledon strands. Its development is slow. Provision is made for the emergence of the first leaf by a cotyledon slit.

Development of Bulb.—On 18th February 1928, when the cotyledons of many seedlings were approximately 4 cm. high, no trace of bulb formation was apparent. Seedlings collected on 17th March had cotyledons 6 cm. high; little in the nature of basal development had taken place, but 1 mm. of the first leaf had emerged through the sheath. Seven weeks later a typical seedling showed, at the base of the cotyledon, a swelling 4 mm. in diameter extending through 6 mm. of the sheath. The cotyledon was then 8 cm. long. The contractile primary root was reinforced by one cauline root.

During the winter the aerial portions of the plant died down. Observations were next recorded on 18th April 1929. The bulb was then 1·5–2 cm. below the surface, the plumular bud being then at the apex of a short conical axis in which the curvature characteristic of leaf traces in Monocotyledons is apparent (fig. 13, ii). The leaf nearest the bud was still within the bulb, surrounded by the bases of two aerial leaves, 17·5 cm. and 10·5 cm. long respectively. The bases of the latter were enclosed by the succulent sheaths of the first leaf and cotyledon.

The floral axis which was produced at the beginning of June 1929 showed at once the climbing habit, twisting spirally and attaining a height of 5 cm. in three days. It

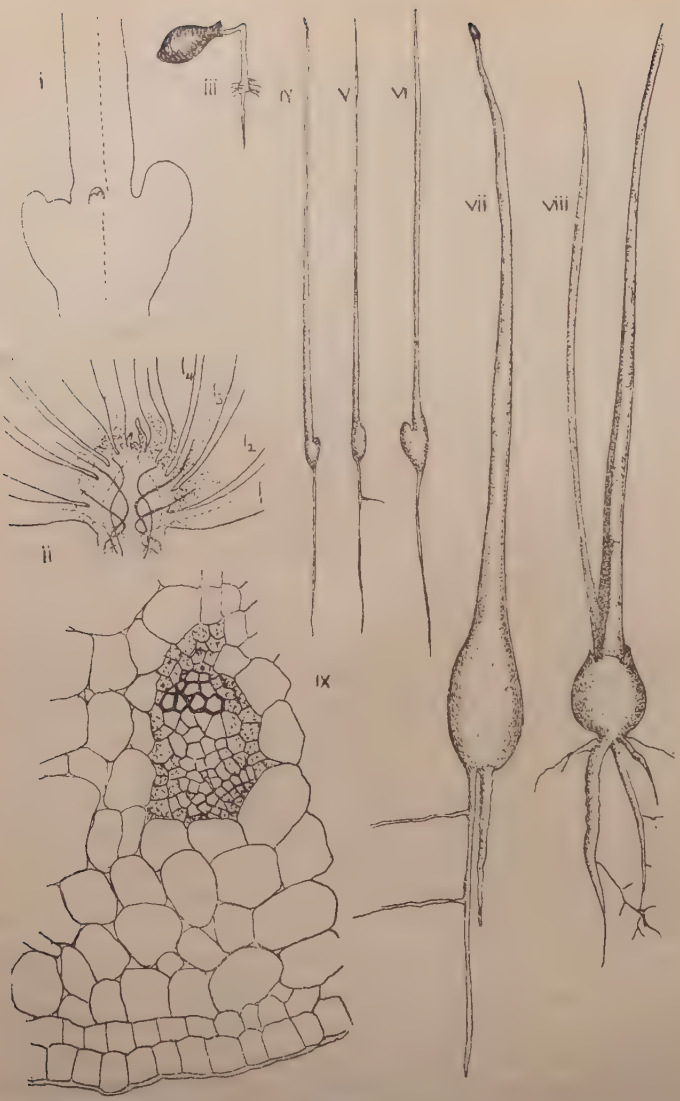

Fig. 13.—*Bowiea volubilis*. i. Longitudinal section of seedling figured in iii, showing the undifferentiated state of the plumule and parenchyma collar round the hypocotyl (× 10). ii. Longitudinal section of bulb of a plant one year old, showing the symmetrical arrangement of leaf traces (l_1, l_2, l_3 = first, second, and third foliage leaves). iii. Seedling three days old (× 2). iv–vi. Seedlings eight, ten, and twelve weeks old (actual size). vii. Seedling six months old ; one adventitious root supplements the primary root (× $\frac{2}{3}$). viii. Plant one year old with the first two foliage leaves ; the bulb is covered by the base of the cotyledon (actual size). ix. Transverse section of fragment of cotyledon lamina, showing one cotyledon strand ; the epidermis is cutinised (× 150).

bore at this stage a terminal bud and two short lateral branches each subtended by a scale. The stem was bright green to within 4 mm. of the base even where encased by the bulb, which was semi-transparent.

At this, the final stage examined, the bulb had a maximum diameter of 1·5 cm., and consisted chiefly of three semi-transparent mucilaginous bases of aerial leaves, each entirely enfolding the underlying leaf-base. Below there arose a

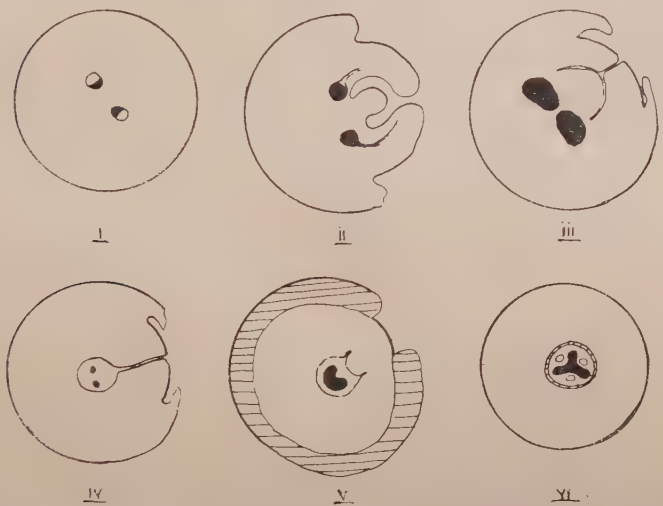

Fig. 14.—*Bowiea volubilis.* Transverse sections of seedling a week old. i. Lamina of cotyledon. ii–iii. Level of the plumular bud, showing the cotyledon slit. v. Hypocotyl showing the parenchyma collar. vi. Primary root.

thinner scale (apparently never possessing an aerial part) and, still nearer the centre, the base of the current year's oldest green leaf, of which a considerable portion of lamina had died back. Its base was not sufficiently wide to encircle the slender scale leaf, the base of the second green leaf and the climbing axis within. Four or five minute colourless scales were arranged in a whorl round the base of the latter, and five long, generally unbranched, contractile roots were placed centrally at the base of the bulb.

Anatomy.—In a seedling a few weeks old two parallel strands pass from the tip of the cotyledon to the base, at which level they converge (fig. 14). Below the plumule they fuse to give a crescent of xylem. Complete fusion of cotyledon and

plumular traces having occurred, the xylem becomes consolidated to a triangular plate which is surrounded by a ring of phloem. Owing to its slow development, the plumule makes an almost negligible contribution to the root stele.

At the level of the plumule a collar of tissue three cells deep, which is piliferous and continuous with the root epidermis, surrounds the margin of the base of the cotyledon. The root stele is typically triarch. A single pericyclic layer is

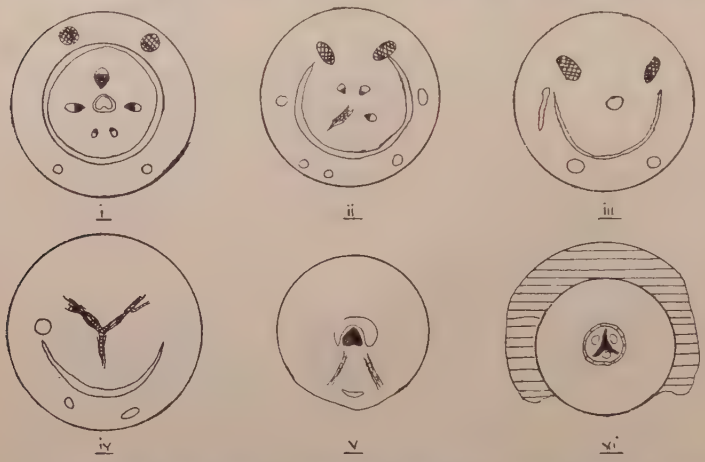

Fig. 15.—*Bowiea volubilis*. Transverse section of seedling three months old. i. Level of plumular bud; original strands cross-hatched. iv–v. Upper limit of hypocotyl. vi. Primary root.

present, but little or no parenchyma. The xylem breaks up into three small groups at the root tip. The triarch root stele clearly consists, in older seedlings, of tissue, two-thirds of which have been contributed by the cotyledon, the remainder coming from the plumule. In the youngest seedling, however, a higher proportion of root stele is cotyledonary in origin; in spite of this, triarchy characterises the early stages. Sargant's observations (120) on other members of the Tribe indicate that cotyledon and plumular traces in the proportions shown by the older *Bowiea* produce triarchy. When fully grown the first leaf resembles the cotyledon in form, length, and succulence. Originally it has five vascular strands, but later ten.

As the plant becomes bulbous, the base of the cotyledon has necessarily to increase in width. In a year-old specimen

two or three additional strands run parallel to the original pair, from which the supplementary bundles and several ramifications arise at right angles as the abrupt increase in girth occurs. They enter the axis and are superposed upon the plumular traces before the latter fuse with the original cotyledonary strands. Older seedlings show the transition described, with the additional complication of the union of the subsidiary strands with the traces of the first leaf (fig. 15).

Lateral roots, and cauline roots from the base of the bulb, are sparingly produced. After a year there may be only three or four roots, but these are thick and strong, and store water in the central cortical zone and the hypodermal layer. The tissues of primary and adventitious roots are identical, save that the stele of the latter may be pentarch or hexarch.

The seedling of *Chlorogalum pomeridianum*, another bulbous type, was described by Sargant (120). Germination is hypogeal. The cotyledon has two vascular strands, and the primary root is tetrarch.

Tribe Scilleae—*Ornithogalum* sp.

The anatomy of the young seedlings of certain species has been described by Sargant (120) and Chouard (31).

Eleven-months-old Seedling. — The only photosynthetic organs are the cotyledon and one or two leaves, the swollen bases of which form the bulb. The cotyledon consists of a much swollen, water-storing sheathing base, approximately 2 cm. long and 7 mm. in diameter, through which pass the two original strands and, in the basal region, two parallel subsidiary strands. The green portion of the cotyledon is cylindrical, 5 cm. long, and is heavily cutinised on the outer epidermal walls. The seed still adheres to the suctorial tip. The first leaf is similar in appearance and length to the cotyledon (fig. 16). In transverse section it is hexagonal. The epidermal cells are elongated radially, with cutinised outer walls; the palisade layer immediately below is one cell, frequently two short cells, deep. One main and two lateral strands lie at the corners of a triangle, in a mass of parenchyma with small intercellular spaces. The primary root is persistent; at an early stage it becomes contractile, and later sends off rootlets. Cauline roots from the base of

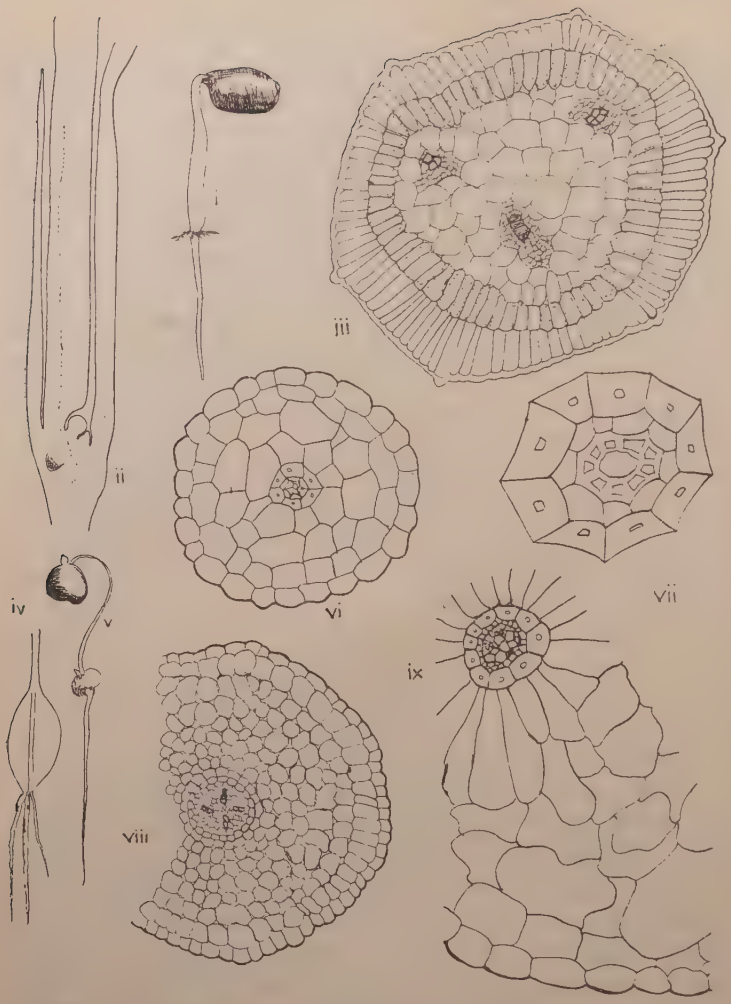

FIG. 16.—i–ii. *Lachenalia* sp. i. Seedling one week old (× 4). ii. Longitudinal section of seedling two weeks old ; the first leaf has ruptured the sheath of the cotyledon and an adventitious root has been initiated (× 9). iii. *Ornithogalum* sp. : transverse section of first leaf, showing the heavy cutinisation of the epidermis and symmetry of the tissues (× 500). iv–ix. *Fritillaria* sp. iv. Longitudinal section through the bulb of a seedling four months old : food storage at this stage is confined to the base of the cotyledon (× 4). v. Seedling six months old : the seed and germinal lid are still attached to the tip of the cotyledon, which is the only green organ of the first season (× 4). vi. Transverse section of primary root of seedling four months old, figured in (iv). vii. Stele of primary root figured in (vi) ; only a small lumen remains in the endodermal cells (× 500). viii. Transverse section of young primary root (× 500). ix. Transverse section of a contractile adventitious root (× 500).

the cotyledon are also produced. The primary root is triarch or tetrarch, but adventitious roots may be tetrarch or pentarch. The stele of all the roots is approximately one-ninth of the total diameter. At the base of the bulb the primary and adventitious roots are embedded in a parenchymatous ground mass, extending through 0·5 mm., possibly the result of the persistence and further development of the " collet " observed by Sargant (120) in the young seedling.

Chouard figures a seedling of *O. flavum* Forsk., stating that it presents in an exaggerated manner the same type of germination as *Merendera Bulbocodium* Ram., possessing a ligulate cotyledon and a well-developed first leaf which is triangular in outline. Its primary root is pierced, and later supplanted by a remarkable adventitious storage root. The nature of the perennating organ and the seedling morphology are, for this genus, unusual.

Lachenalia sp.

Germination is hypogeal (fig. 16). The cotyledon consists principally of a tubular sheath ; a very short stalk connects the sheath and suctorial tip. The first leaf rapidly elongates. The length of the persistent primary root corresponds roughly to that of seedling above ground. A ring of strong root hairs occur at its upper limit. A cauline root arises in alignment with the plumule during the first week.

Anatomy.—The cotyledon has a double bundle and two lateral strands. The traces of the first leaf and cotyledon unite immediately below the plumular bud. The anatomy agrees with that of *L. Nelsonii* (120), but the root of the latter is diarch, whereas it is triarch in the species examined.

Muscari.

Seedlings of *M. conicum* and *M. Mordoanum* were examined. In each species germination is epigeal. The cotyledon has two main and two weaker strands, and the long, tapering primary root is tetrarch.

Sargant (120) found this cotyledon anatomy in *M. atlanticum*, which has a pentarch root stele, and in *M. armeniacum*, in which the root is tetrarch. She notes that *M. neglectum* Guss. (which has also a tetrarch root) has two main and four or

more lateral strands in the cotyledon. Chouard (31) refers to the germination of the latter and of *M. racemosum* Mill, *M. botryoides* Mill, and *M. Argaei* Hort.

Other Genera of the Scilleae described in Literature.

Schlickum (127) completely investigated the anatomy of *Hyacinthus candidans*, in which germination is epigeal and there are two strands in the cotyledon. Sargant (120) described the transition anatomy of species of *Albuca*, *Galtonia*, *Dipcadi*, *Hyacinthus*, and *Scilla*, and others already referred to, finding in each epigeal germination, two strands or a double bundle (frequently accompanied by lateral strands) in the cotyledon, and diarchy, triarchy, or tetrarchy of the primary root. Chouard (31) describes the seed, germination, and seedling anatomy of certain types in the tribe and divides the seedlings into two main types—the *Endymion* type having hypogeal, the *Scilla* type having epigeal germination. Plumular development is more rapid in the former. The cotyledon in each type has two vascular strands. A comparison is made between the cotyledon of the *Scilla* type and the first leaf, and between the cotyledon of the *Endymion* type and the scale leaf of an adult bulb. A key, taking into account divergences from the two main types, caused by variation in length of the sheath and rate of germination, is given for the tribe. A third type in which the cotyledon is ligulate contains only *Ornithogalum flavum* Forsk.

Tribe Tulipeae—*Lilium*.

The anatomy of two species (*Lilium monadelphum* var. *szovitzianum* and an unnamed species) was completely investigated and found to be identical. Longitudinal sections of *L. Martagon* were also examined.

The flattened seed (5–7 mm. long) has a thin, black seed coat. Germination is epigeal (fig. 17). Reserve food is stored in the sheathing base of the cotyledon. The plumule is effectively protected by the latter, the margins of which overlap. The cotyledon sheath narrows to a stalk of equal length, merging into an expanded lanceolate lamina, which develops as the suctorial tip is withdrawn from the seed. The plumular bud is strong, but slow in development. The first leaf

possesses three main strands. Internodes are practically suppressed. By the time the first leaf is above the soil the

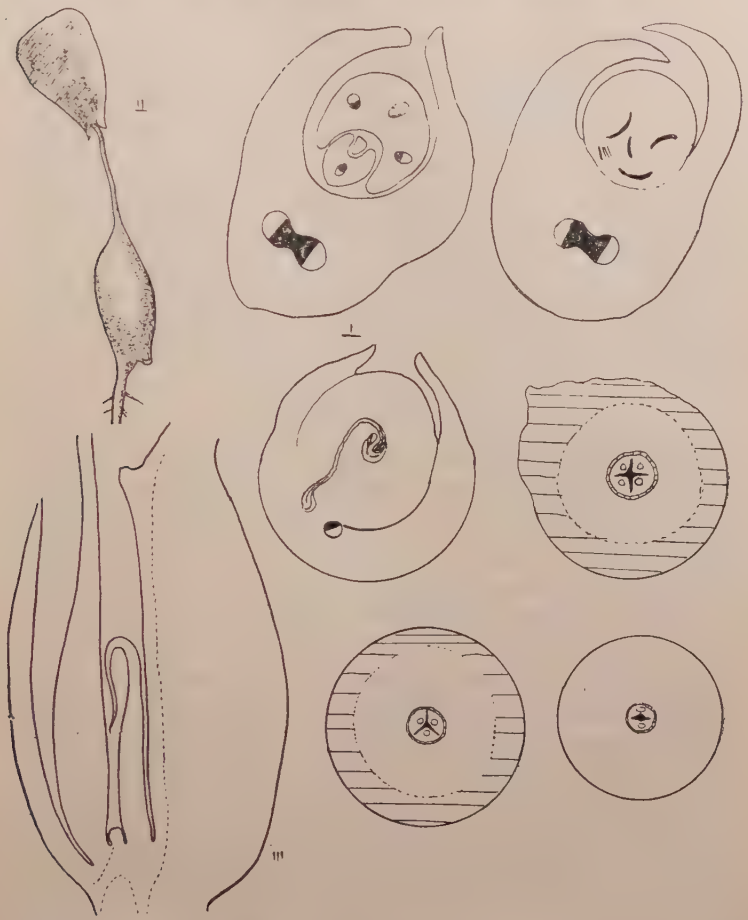

FIG. 17.—*Lilium monadelphum*. i and succeeding transverse sections are of a seedling three weeks old, from the level of the plumular bud to that at which the primary root becomes diarch. ii. Seedling four weeks old (× 3). iii. Longitudinal section of seedling, showing the emergence of the first leaf through the cotyledon sheath (× 14).

primary root, which is persistent, is supplemented by adventitious roots.

Anatomy.—The seedling agrees with other species of *Lilium* (120) in having a double bundle extending from the tip of the cotyledon to its base, the parenchyma of which is storage

tissue. The strand of the cotyledon passes swiftly, but in two portions at slightly different levels, to fuse with the traces from the first and second leaf. At the base of the cotyledon the diameter of the seedling is at its maximum. The hypocotyl does not appear as a distinct region. The upper part of the root is embedded in the parenchyma of the cotyledon. As the girth of the root decreases, and all traces of cotyledonary storage cells disappear, the strongly lignified root stele changes from a typically tetrarch to a triarch plan. At a slightly lower level two protoxylem arms fuse and the root structure becomes diarch.

Sargant examined *Lilium* sp., *L. Henryi*, *L. croceum*. Each has a double trace in the cotyledon and a transition similar to that of *Tulipa*.

Nomocharis pardanthina.

Seed, germination, and seedling resemble those of *Lilium*. The cotyledon of the young seedling is a delicate cylindrical organ. The primary root in the early stages is also very weak.

Anatomy.—There is a double bundle in the cotyledon. Four or five xylem elements are disposed in the strip across the small stele in the primary root.

A seedling six weeks old shows the first sign of bulb formation by the noticeable swelling of the base of the cotyledon. At this stage the cylindrical lamina of the cotyledon becomes more flattened, although not so pronouncedly as in *Lilium*.

Fritillaria sp.

Sargant described the anatomy of *F. imperialis*. It follows that of *Lilium* in having two cotyledon traces inserted on those of the plumule at the first node where the transition begins. She explained the occurrence of tetrarchy or hexarchy in the primary root as being due to its persistence (120).

In a young seedling of the species examined the tetrarch primary root has an exodermis of very large cells (fig. 16, viii). A year-old seedling has no foliage leaf, although the first leaf is growing out through the cotyledon sheath. The aerial portion of the cotyledon is cylindrical, carrying the seed at its tip, and the base has swollen to form the small bulb, which

is pulled deeper by the contractile primary root. The structure of the primary root stele is consistent with its lengthy function, each endodermal cell being so strongly suberised that only a very small lumen remains (fig. 16). Of the original tetrarch symmetry no trace is left, for the xylem consolidates to a strong hollow cylinder which is separated from the endodermis by a pericycle of large, thin-walled cells.

References in Literature to other Genera of the Tulipeae.

Sargant (120) comments on the uniformity in the anatomy of the tribe. In addition to *Fritillaria* she examined two species of *Tulipa* and a species of *Erythronium*. Robertson (115) described the formation of droppers in *Erythronium* and *Tulipa*. The latter conforms to the double-bundle type with diarch root ; the dropper is cotyledonary in origin and supplied by branching of the cotyledon strand. Robertson regarded triarchy in the root of *Erythronium* as a necessity, since the plant is dependent upon it for a considerable period. (Sargant accounted for the aberrant seedling anatomy by the early transformation of the first leaf to a dropper.) A fuller account of the dropper of *Erythronium* is given by Blodgett (13), who indicates that in the first instance it is not plumular but cotyledonary. He describes *E. americanum*, which has two vascular strands in the cotyledon, the latter functioning as the only photosynthetic organ of the first year. The delayed germination is correlated with the large store of endosperm, and the development of the primary root with the exhaustion of the reserve. The brief period of vegetative activity is believed to be an adjustment to short growing seasons.

Seedlings of other Bulbous Genera.

The seedlings of six species of *Allium*, *Bloomeria aurea*, and *Milla biflora* (Allieae) were examined by Sargant (120). The *Allium* species have a double bundle, *Bloomeria* two strands, in the cotyledon ; the primary root in each is diarch. The transition anatomy is alike save in *Milla*, which has a triarch root. Schlickum (127) has described the anatomy of *Allium fistulosum*.

Amaryllidaceae.

When the seeds of Amaryllidaceae are numerous they are small, flattened, and winged, but when few they are large, green, and irregular or bulbiform in shape.

Schlimbach (128) finds in the seed and embryo a wide range of characters. The majority of seeds have a high water content (*Crinum*, 92·9 per cent. ; *Haemanthus*, 86·3 per cent.), which is correlated with a starchy endosperm and small, poorly differentiated embryo, requiring some time for after-ripening. A well-differentiated embryo is found in seeds having a low water content and oily endosperm. Rendle (110) remarks that the type of germination for the family is the same as for Liliaceae. The bulbous types in their germination resemble the seedlings just described.

Group I. (Seeds Numerous.)

Hippeastrum.

Three species, *H. advenum*, *H. bicolor*, and a hybrid from two unknown species, were examined.

The seed is light in weight, flat, covered with a black papery testa, and approximately 1 cm. in length.

Germination is hypogeal. The cotyledon has a somewhat lengthy tubular sheath. After a few days the short primary root elongates rapidly, keeping pace in growth with the cotyledon ; it is persistent, increases in girth in the upper part for water storage, and later becomes contractile. The sheath elongates considerably before the first foliage leaf emerges through the cotyledonary slit, which it does in a week or so. A distinct swelling of the cotyledon sheath at an early stage gives a bulbous appearance to the young plant.

Anatomy (fig. 18).—The ground tissue of the cotyledon is water-storing and mucilaginous. A pair of vascular strands proceeds from the tip to the base, turns abruptly inwards, and fuses with the plumular traces. The first leaf has a mid-rib and a pair of lateral strands. The primary root is triarch at the upper limit, two-thirds of the stele being derived from the strands of the cotyledon. As it tapers to the tip its stele becomes diarch, and finally the xylem is reduced to a few elements. The cortex is enclosed by a double layer

of large, squarish cells which may be termed a multiple piliferous layer, or velamen.

Anatomically *H. bicolor* showed differences in the structure of cotyledon and root. The cotyledon was supplied by three

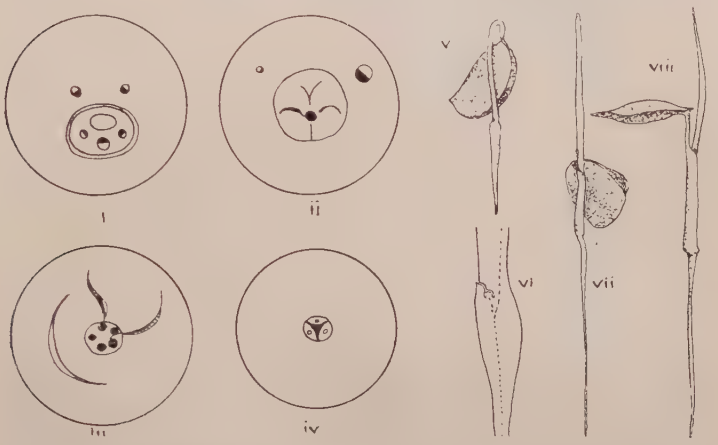

Fig. 18.—i–iv. *Hippeastrum X.*: transverse sections from the cotyledon sheath and base of the first leaf (i) through the hypocotyl (iii) to the primary root. v. *Hippeastrum advenum*: seedling a week old (actual size). vi. Longitudinal section of seedling a week old, showing the weak plumular development (× 10). vii–viii. Seedlings of *Hippeastrum bicolor* (actual size).

strands which might be regarded as a mid-rib and two lateral strands, the latter derived, for no apparent advantage, from the splitting of a single strand, while the primary root is tetrarch and not triarch.

Zephyranthes sp.

Zephyranthes (fig. 19) resembles *Hippeastrum bicolor* in germination and in seedling form and anatomy. The first leaf is almost cylindrical; it has a mid-rib and a pair of lateral strands, but the number of strands increases to five at the widest part of its sheath.

Narcissus.

Anatomy, germination, and seedling (fig. 19) as for *Hippeastrum.*

Narcissus Eglintoni.—Like *Agave,* there are two strands in the suctorial tip of the cotyledon and an extra pair of

subsidiary strands in the sheath. The primary root, which is tetrarch, has a piliferous layer of small cells and an exodermis of very large, squarish cells. The prominent central bundle of the first leaf is surrounded by eight small peripheral strands.

Narcissus Bulbocodium.—The cotyledon has a single vascular strand, the first leaf a mid-rib and a pair of lateral strands. The primary root is diarch.

Pancratium.

Three species were examined, namely, *P. foetidum*, *P. maritimum*, and *P. canariense*. Young stages of the latter were not obtained.

Pancratium foetidum (fig. 19) resembles *Narcissus Eglintoni* in germination, morphology of seedling, and anatomy of cotyledon and root. The four xylem rays meet in the centre of the root stele instead of being peripheral as in *Narcissus*. The first leaf has a mid-rib and two lateral strands.

Pancratium maritimum (fig. 19).—Two strands are found in the cotyledon, but throughout most of the sheath one strand is composed of two distinct xylem traces. The primary root is tetrarch, the four xylem groups being peripherally arranged in the stele. The sheath of the first leaf has an additional pair of lateral strands.

Pancratium canariense.—The seedling examined was three months old. Only a thin, papery fragment of cotyledon remained, wrapped round the swollen bases of the first two foliage leaves. Two cotyledon strands could be distinguished, but it was impossible to determine whether subsidiary strands had been present. The first leaf had ten vascular strands in the sheath, which was a hollow cylinder enclosing the base of the second leaf; the latter had five vascular strands. The base of the long bulb consists of a ground mass of storage tissue, welding together three roots, one the original tetrarch root of the young seedling, the others polyarch. The primary root has a remarkably strong endodermis, which is further fortified by thickening of the innermost cortical layer.

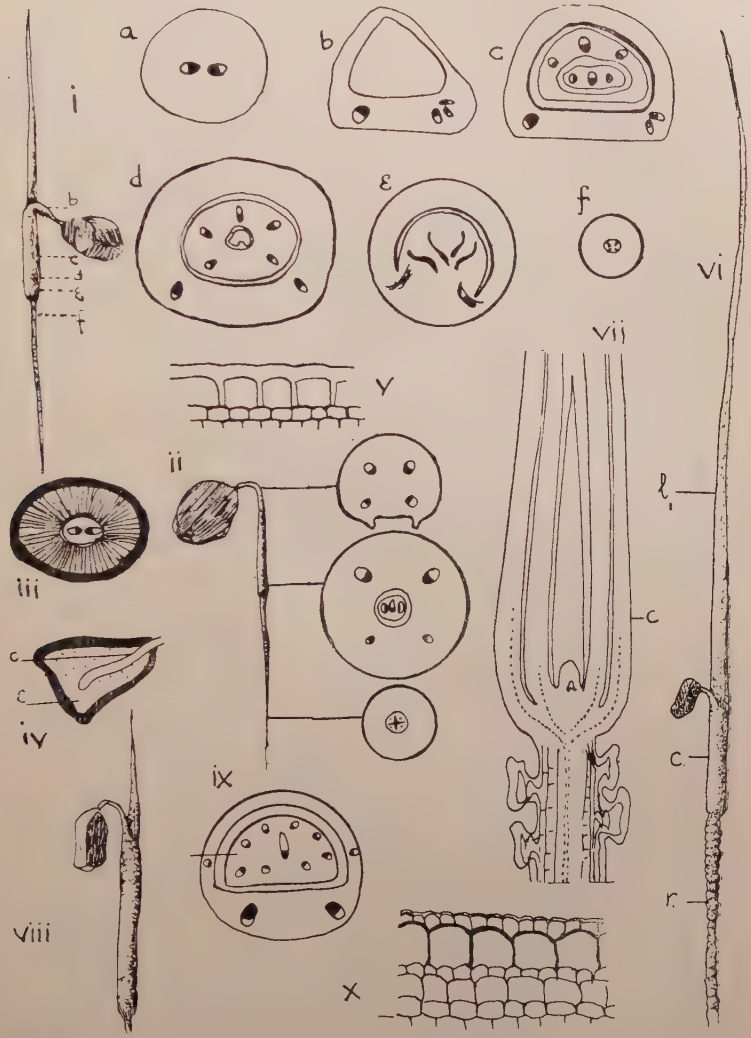

Fig. 19.—i. *Pancratium maritimum*: young seedling (×2); *a–f*, transverse sections at levels marked. ii. *Pancratium foetidum*: young seedling (×2) and transverse sections at indicated levels. iii–v. *Pancratium maritimum*. iii, iv. Longitudinal and transverse sections of seed, showing suctorial tip (*c*) in endosperm (*e*). v. Cutinised epidermal cells of cotyledon. vi. Seedling of *Zephyranthes* sp. (l_1=first leaf, *c*=cotyledon, *r*=primary root). vii. Longitudinal section of part of seedling figured in vi, showing contractile primary root. viii–ix. *Narcissus Eglintoni*. viii. Young seedling (×2). ix. Transverse section through cotyledon sheath and base of first leaf.

Group II. (Seeds Few.)

The seeds are among the largest encountered in this study. Although bulky, they are not necessarily heavy. Their true nature was the subject of considerable discussion which Rendle (109) has summarised. He divides them as follows :—

A. (i) The bulbiform mass is derived from the outer integument, e.g. *Hymenocallis.*

(ii) The seeds are naked ovules, the endosperm providing the fleshy substance, e.g. *Crinum.*

B. A bulbil is formed before germination to replace the seed, e.g. *Calostemma.*

Brunsvigia.

Brunsvigia sp. K. 59 (from the Drakensberg).

A month after germination the seed is somewhat shrivelled (fig. 21, viii). It consists of a fleshy spherical mass of parenchyma, approximately 12 mm. in diameter, covered with periderm four cells deep ; there is no true testa.

Germination is Type B. The bulky cotyledon has a conspicuous sheath which in a few weeks may be 2·5 cm. in length and 0·5 cm. in diameter. The stalk connecting sheath and seed may itself be 1·5 cm. The plumule is carried downwards into the soil by the elongating sheath. The persistent primary root is long, tapering, and succulent.

Anatomy.—The massive character of the seed and seedling finds an expression in the anatomy. In the suctorial tip of the cotyledon, which occupies one-third or half of the seed and is 2–4 mm. in diameter, there are nine strands, each enclosed in a firm parenchymatous sheath. Ramifications are rare. Towards the extreme tip the strands fuse in pairs, which converge in the centre. There are nine strands in the cotyledon sheath, the ground tissue of which is mucilaginous. The primary root has a small-celled epidermis from which root hairs are noticeably absent, an exodermis of large cells, a wide water-storing cortex, and a strong stele with ten protoxylem groups and metaxylem scattered irregularly towards the centre (fig. 21, xi). The first and second leaves have four pairs of lateral traces, arranged round a mid-rib.

Brunsvigia sp. K. 64 is similar, but its root is hexarch, and the cotyledon has six traces in the sheath, with the outermost

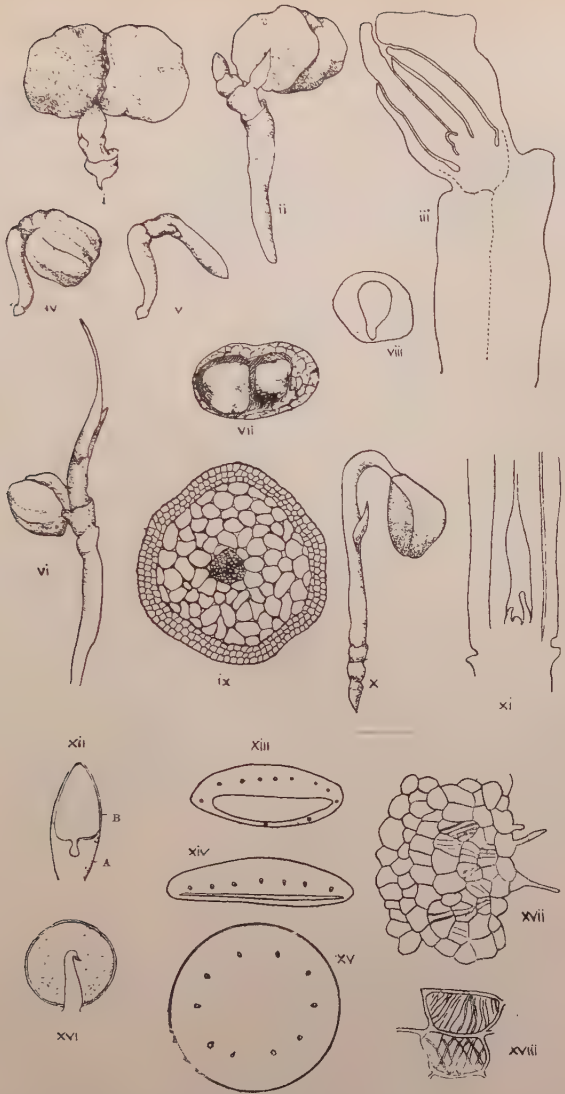

FIG. 20.—i–iii. *Clivia miniata*. i. Seedling four days old ($\times \frac{1}{2}$). ii. Same seedling a month later; the seed has cracked but the tip is still embedded in endosperm. iii. Longitudinal section of seedling in ii ($\times \frac{5}{2}$). iv. Seedling of *Clivia* sp. 101 ($\times \frac{1}{2}$). v. Seedling figured in iv, with suctorial tip dissected out from seed ($\times \frac{1}{2}$). vi. Older seedling of *Clivia* sp. 101 ($\times \frac{1}{2}$). vii–viii. *Clivia miniata*: fruit with two ovules. viii. Longitudinal section of seed, showing embryo ($\times \frac{1}{2}$). ix–xi. *Haemanthus* sp. ix. Transverse section of primary root ($\times 20$). x. Young seedling ($\times \frac{2}{3}$). xi. Young seedling in longitudinal section ($\times 10$). xii–xviii. *Clivia miniata*. xii. First leaf (actual size). xiii. Transverse section of first leaf at A ($\times 3$). xiv. Transverse section of first leaf at B ($\times 3$). xv. Transverse section of cotyledon sucker where it enters the seed ($\times 10$). xvii. Fragment of cortex and piliferous layer of the primary root in transverse section ($\times 10$). xviii. Reticulate cells in the velamen of the primary root.

pair ramifying at the base. The seedling is smaller than that of *Brunsvigia* sp. K. 59 of the same age.

Longitudinal sections of *B. gigantea* show the general structure described for the above species. The poor development of primary root in the seedlings (self-germinated) is conspicuous.

Clivia.

Clivia miniata and an unnamed species (*Clivia* sp. K. 101) were examined.

Clivia miniata.—The hemispherical seed is larger than that of *Brunsvigia* (fig. 20), and consists of firm fleshy tissue protected by a thin brown covering which readily peels off. At germination the seed becomes pale green.

Germination is hypogeal. The cotyledon, which has a shorter sheathing base (less than 5 mm.) than in *Brunsvigia*, lacks the lengthy stalk, connecting sucker and base. From the initial stage the primary root, which has a blunt conical tip, is strong. The plumular bud appears in a few days as a short lateral outgrowth. The seed from this period may be raised upwards through the soil, by the vigorous growth of root and cotyledon sheath. The emergence and subsequent expansion of the plumular bud causes the seed to crack. The first plumular organ produced by *Clivia* is a short, clasping leaf (fig. 20, xii). The true foliage leaf succeeds it, appearing one month after germination.

Anatomy.—The cotyledon has ten vascular strands throughout its length. The primary root stele has approximately ten xylem rays, and is surrounded by a wide cortex, a thin-walled exodermis, and a velamen. Almost every cell of the latter is reticulate. The *first leaf* has nine parallel strands, a number which is increased to thirteen towards its base.

Clivia sp. K. 101 has a slightly smaller seedling than *C. miniata*. The seed is the same size as that of *Brunsvigia*. The seedling differs anatomically from *C. miniata* in having only six vascular strands in the cotyledon, and showing heptarchy in the root, which has the same type of cortex, exodermis, and velamen.

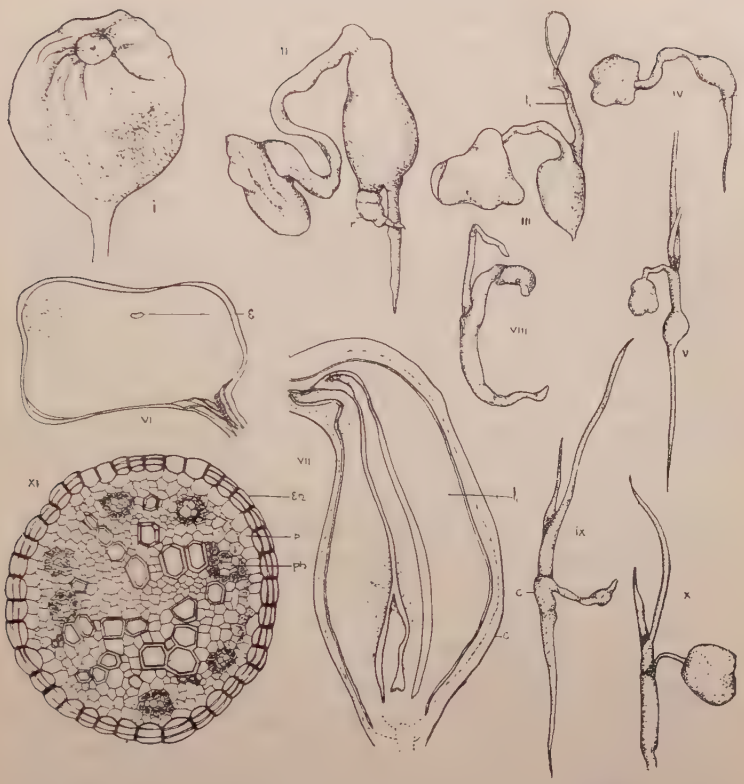

FIG. 21.—i. Seed of *Crinum Macowani* ($\times \frac{1}{2}$). ii–iii. Young seedlings of *Crinum* sp. K. 34 (actual size). iv–v. Young seedlings of *Nerine Bowdeni* (actual size). vi. Seed of *Crinum Macowani* in longitudinal section, showing embryo (*e*) and tracheids in the stalk. vii. Longitudinal section of seedling of *Crinum* sp. figured in iii. viii–x. Seedlings of *Brunsvigia* sp. ($\times \frac{1}{2}$). xi. Transverse section of the stele of the primary root ($\times 100$).

c = cotyledon ; *en* = endodermis ; l_1 = first leaf ; *p* = pericycle ; *ph* = phloem.

Crinum.

Two seedlings of an unnamed *Crinum* (K. 34) and the embryos of *C. Macowani* and *C. giganteum* were examined.

Crinum Macowani.—The truly remarkable seed of *Crinum* has been previously discussed, but, as in the case of other members of this group, no anatomical details of the seedling are available. The seed of *C. Macowani* is soft and light, fig-shaped, and approximately 6 cm. long. The spongy, pale

green endospermic mass is surrounded by a network of strong tracheids and spirally thickened vessels, which proceed from a stalk, doubtless the original funicle. They were recorded by Braun (17) as being in the fleshy mass, but correctly by Salisbury (117) as entering at the hilum and distributed round the margin. The embryo is ovoid or cylindrical (fig. 21, vi) and of large dimensions, being 3–6 mm. in length. Its greatest bulk consists of the cotyledon, which in the ripe embryo is supplied by twenty-six vascular strands. The young embryo clearly shows the lateral origin of the plumule, but the latter is so massive in the mature embryo (five leaves being differentiated) that it occupies a median position. The ripe embryo therefore appears symmetrical. The first leaf has twenty-four to twenty-six strands and the primary root is polyarch (eight or ten poles). The embryo of *Crinum giganteum* is equally well differentiated.

Crinum sp. K. 34.—The seed resembles that of *C. Macowani*, but is much smaller and has an average length of 15 mm.

Germination is Type B. The cotyledon is peculiar in certain respects. The well-developed sheath, which soon becomes greatly swollen, differs in length according to circumstances. (This was earlier observed by van Hall (64), who figured a seedling of *Crinum capense* which germinated on the edge of a board and showed an exaggerated development of the sheath. Beaurieux (8) has made a detailed study of the physiology of germination of the same species.) The stalk region, which is unusually thick, twists in an irregular fashion, its long meandering course recalling, on a smaller scale, the germination of the double coco-nut, *Lodoicea sechellarum* Labill (142). Fischer (48) referred to it as a "worm-like elongation." According to Salisbury (117) no law governs the point of emergence of the original process from the bulbiform seed. Worsley (157) therefore correlates the curvature of the stalk with the necessity for chancing upon a downward direction, but it seems difficult to explain the unnecessarily large number of twists. The twisting of the stalk finds a repetition in the behaviour of the finger-like or club-shaped tip which may bend in the endosperm in any direction. This has been figured by at least two authors (2, 117).

Anatomy.—The cotyledon has six strong vascular strands in the tip and stalk. The number increases to ten in the

swollen sheath. There are a mid-rib and two pairs of lateral strands in the first leaf. The multiple piliferous layer of the primary root consists of reticulately thickened cells, and the stele is hexarch.

The seedling seems to be in a certain degree independent of the primary root, the development of which is unexpectedly weak. Worsley (157) observes that in *C. Moorei* there may be no sign of root " until the seed is quite dead and the bulb is formed " (three months after germination), when several roots are produced simultaneously.

Haemanthus sp. (K. 92).

The seed is pear-shaped and approximately 1 cm. in length. The germination and seedling (fig. 20) are similar to what have been described for *Clivia*.

Anatomy.—There are six strands in the cotyledon, which is a succulent organ forced to widen to accommodate the swollen leaf bases of the plumule. The first leaf has eight strands. The short primary root is thick, succulent, and contractile from an early stage; the stele is tetrarch, the cortex wide and mucilaginous, and there is a multiple piliferous layer, three cells deep (fig. 20). The fact that the primary root remains relatively short was observed by Klebs in *Haemanthus puniceus*; it is also true for *Amaryllis*.

Nerine Bowdeni.

The seed is spherical, the diameter being less than 1 cm. It is soft, fleshy, and chlorophyllous, protected by a thin layer of periderm. Schlimbach (128) comments on the stomata in the covering layer. The small, poorly differentiated embryo is surrounded by starchy endosperm.

Germination is Type B. The cotyledon stalk in certain instances shows the vermiform convolutions and elongation observed in *Crinum*. The seedling is comparable to *Haemanthus* with regard to bulk, if seedlings of the same age be considered, but the primary root of *Nerine* is less well developed (fig. 21).

Anatomy (fig. 22).—The cotyledon and first leaf have the same venation, namely, a mid-rib and two pairs of lateral

strands. At the base of the cotyledon sheath its mid-rib divides, one-half fusing with each of its two adjacent lateral strands. The cotyledon strands enter the central axis at different levels, giving the appearance of a slow transition,

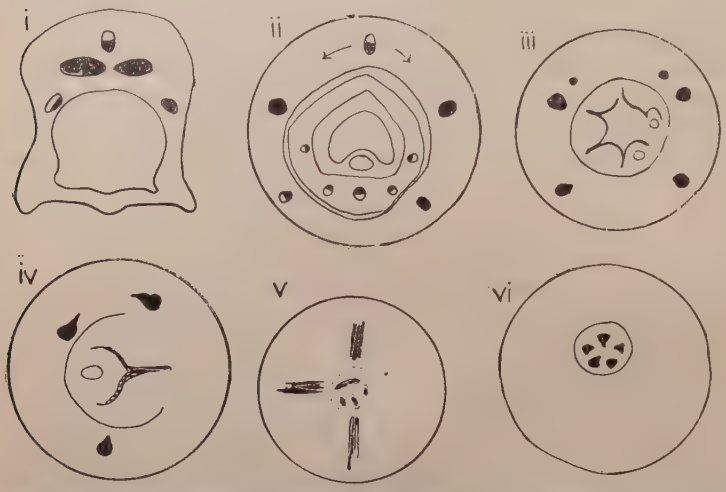

FIG. 22.—*Nerine Bowdeni*. Transverse sections of a seedling before the first leaf has emerged from the sheath. i. Cotyledon sheath. iii. Base of the first internode. iv–v. Upper limit of hypocotyl. vi. Primary root.

although, externally, no hypocotyl can be distingished. The primary root, which is pentarch and has a much-swollen exodermis, becomes contractile.

Carpolyza spiralis.

The large, ovoid seed (1 cm. by 2·5 mm.) is covered by a layer of small, thin-walled cells, interrupted by stomata. The embryo, a straight body 2 mm. in length lying at the narrow end of the seed, resembles the embryo of *Crinum*. The plumular bud is large, but relatively undifferentiated. Germination was not followed.

Ixiolirion tataricum.

The embryo is cylindrical and straight (5 mm. by 0·5 mm.). The first leaf in the mature embryo may be more than 1 mm. in length ; the second leaf is then not distinctly differentiated

from the plumular bud. Data for germination are not available.

References in Literature to other Genera.

The only additional account found of the early life of a bulbous plant of Amaryllidaceae is given by two authors (47, 141) describing *Cyrtanthus*. From observations of the development and anatomy of the cotyledon in the embryo of *C. sanguineus*, Farrell (47) concluded that the cotyledon sheath in monocotyledons is a fusion of two or more seed leaves, but Taylor (141) found the cotyledon of *C. parviflorus* to be a normal terminal structure and the seedling anatomy easily connectible with Sargant's Amaryllidaceous types.

Summary.

Bulb formation is apparent within the first two months of life, the sheathing base of the cotyledon forming the outermost scale of the bulb.

The strong primary root common to all may function alone for a year. The production of adventitious roots is strictly limited, and root hairs appear sparingly. During the first year only one cauline root, as a rule, appears. For the purpose of securely fixing the bulb in the soil, the primary root becomes contractile. In each case there is modification of the cortex for water storage; the second group of the Amaryllidaceae shows further elaboration in the form of an enlarged exodermis, or multiple piliferous layer or velamen. The continued elongation of the primary root is doubtless related not only to its contractile function but to the habit of plants which are specialised for unfavourable conditions and require deep-boring roots.

The absence of a hypocotyl contrasts with its development in species of different habit in Liliaceae and Amaryllidaceae. *Doryanthes*, for example, an Amaryllidaceous arborescent plant, has a lengthy hypocotyl. Since the plumule is below the surface and tends to be pulled deeper, hypocotylar elongation in the bulbous plant would be superfluous.

Heavy cutinisation of the epidermis of the cotyledon and foliage leaves for the conservation of water occurs in all species examined.

The cotyledon may be epigeal and have a cylindrical or flat blade, the lamina of the cotyledon and first leaf then bearing a general resemblance to each other. In certain instances (for example, *Bowiea*) it is the only assimilatory organ for the first year. Chouard (31) notes this type as characteristic of *Scilla*, *Muscari*, *Bellevalia*, and *Hyacinthus* in the tribe Scilleae. On the other hand, if germination is hypogeal the first leaf develops more rapidly. The tubular cotyledon sheath may be short (as in the majority of the species quoted) or relatively long. The hypogeal cotyledon is morphologically similar to the epigeal type. In preserved material where the plants have lost their chlorophyll it may be a little difficult to decide to which type the very young seedling belongs. Instead of elongating to carry the seed upwards, the hypogeal cotyledon assists the primary root to bore more deeply into the soil. The abnormal activity of the stalk portion of the cotyledon in certain Amaryllidaceae is noteworthy.

The main differences are revealed by the anatomy. The Liliaceae considered have two strands in the cotyledon (except *Erythronium*, which may have three), and the root stele is di-, tri-, or tetrarch, pentarchy being unusual. Such uniformity is not shown by the vascular anatomy of Amaryllidaceae, as the following summary shows :—

Table I.

	Cotyledon.	First Leaf.	Primary Root.
Hippeastrum X . .	2 strands	3 strands	3-arch
,, *bicolor* .	3 ,,	3 ,,	3-arch
,, *advenum* .	2 ,,	3 ,,	3-arch
Narcissus . . .	2, +2 laterals	1, +8 laterals	4-arch
Pancratium foetidum .	2, +2 ,,	3 strands	4-arch
,, *maritimum* .	2 strands	3 ,,	4-arch
Zephyranthes sp. . .	3 ,,	3 ,,	3-arch
Brunsvigia sp. K. 64 .	6 ,,	9 ,,	6-arch
,, sp. K. 59 .	9 ,,	9 ,,	10-arch
Clivia sp. K. 101 . .	6 ,,	9 ,,	7-arch
,, *miniata* . .	10 ,,	9 ,,	10-arch
Crinum sp. K. 34 . .	6 ,,	5 ,,	6-arch
,, *Macowani* .	26 ,,	24–26 ,,	10-arch
Haemanthus sp. . .	6 ,,	8 ,,	4-arch
Nerine Bowdeni . .	5 ,,	5 ,,	5-arch

Seedlings with two or three strands in the cotyledon and triarch or tetrarch roots belong to Rendle's first group, in which the seeds are numerous and small. They are comparable to the hypogeal seedlings of the Liliaceous group not only in anatomy but in their external morphology, the size and appearance of seed and seedling being so much alike that they are difficult to distinguish from Liliaceous species. Large, fleshy, bulbiform seeds, equipped for rapid germination, produce seedlings with an internal structure corresponding to a development, on a large scale, of embryo, cotyledon, and plumule. The numbers more than suggest the intimate relation between root and cotyledon, which is scarcely influenced by fluctuation in the number of first leaf vascular strands. While the latter will undoubtedly affect the strength of the root stele, their presence does not seem to disturb its symmetry, as determined by the cotyledon.

The habitat is presumably somewhat similar for the seedlings, since they have been chosen as showing a similar response to it—namely, the bulbous habit. The influence of the habitat ought, then, to act more or less uniformly on all. Consequently the difference in anatomy between the two groups may be referable to a variable factor, such as the size of the seed and adult plant. The Amaryllidaceae exemplify a correlation between the external and internal morphology of the seedling and size of the seed.

B.—Plants producing Corms and Tubers.

No distinction was made between corm and tuber. In the Iridaceae the term corm is given to the perennating body, which is renewed annually. The name tuber is commonly used in the Aroideae, although several writers apply the word corm to the underground organ of *Arisaema*.

Liliaceae.

Tribe Colchiceae—*Merendera Bulbocodium* Ram.

The seed is endospermic ; its length is approximately 3 mm.

Germination is Type C (fig. 23). In a young seedling the cotyledon consists of a narrow sheathing base approximately 2 mm. long, and a ligule about nine times as long as the sheath.

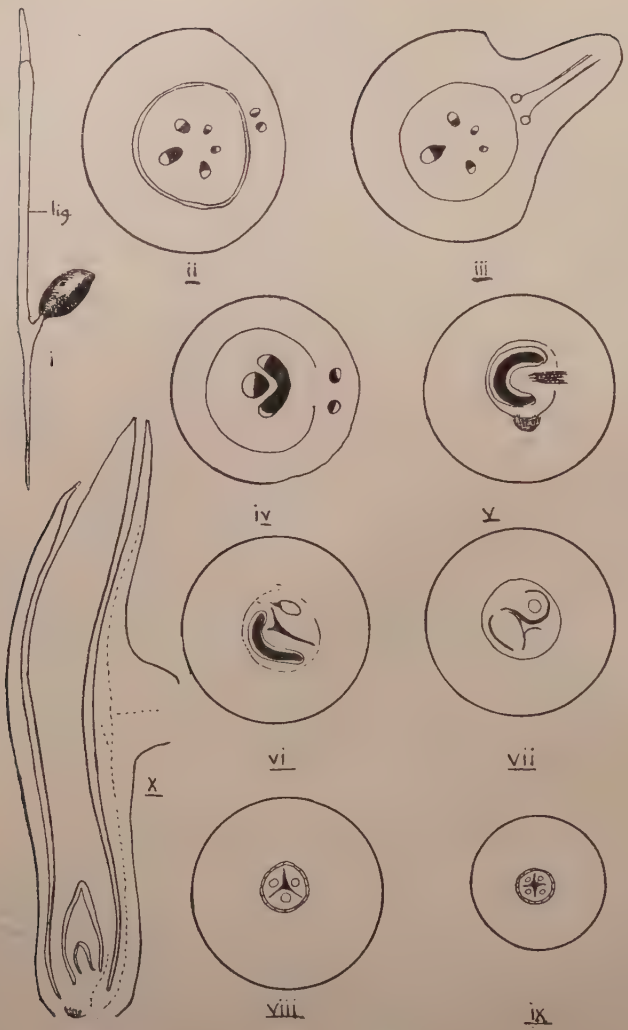

Fig. 23.—*Merendera Bulbocodium.* i. Seedling showing the first leaf appearing through the apex of the pronounced ligule (*lig*) (× 2). ii–x. Transverse sections of seedling figured. ii. Ligule and first internode. iii. Passage of cotyledon strands from the sucker. v. Upper limit of hypocotyl. vi–vii. Hypocotyl. viii. Upper limit of primary root. x. Longitudinal section of seedling at the same stage of development as in i, showing the course of the cotyledon strands and the initiation of an adventitious root (× 20).

A very short stalk ($\frac{1}{2}$ mm. in length) connects with the cylindrical suctorial tip, which is approximately the same length as the seed. The plumule is well developed. The first leaf, which is long, narrow, and cylindrical, has a strong mid-rib and two pairs of lateral strands. The outer pair of laterals fuse together at the base of the leaf, the other strands remaining distinct until the transition. Internodes in the seedling are very short and a hypocotyl is absent. The strong, persistent primary root, which lengthens more slowly than the aerial organs, is early reinforced by cauline roots and becomes contractile.

Anatomy.—Two strands with protoxylem almost touching run from the tip of the cotyledon through the stalk (fig. 23). Each branches, sending a weak strand vertically upwards through the ligule, and a strong strand vertically downwards. The two downward strands move towards the plumular traces when the latter are reduced to three. An arrangement of five distinct traces continues through 70 μ. The transition is swift, occurring within 80 μ, and results in a triarch root stele.

The seedling of *Colchicum autumnale* L. (described by Sargant and Arber) (124) shows an almost identical structure. Fabre (46), who gives no anatomical details, describes the swelling of the upper part of the primary root in this genus. The corm is evidently produced by a lateral swelling of the hypocotyl, but the epidermis of the top of the root and the base of the cotyledon protect it; the continued growth of the corm destroys the cortex of the root in its neighbourhood. The elongation downwards of the starch-filled conical body, and the origin of a bud arising laterally in the basal part of the corm, are described. The bud for the next year is carried deeper in the soil by the asymmetric growth of the current season's corm, the roots taking no part in the process. Rimbach (114) has commented on this unusual method of fixing the corm more deeply each year. Two months or so after germination connection with the cotyledon is broken, and, though the cortical tissue of the primary root disappears, its epidermis and vascular tissue persist, forming part of the corm's protective sheath. When the cotyledon shrivels up, the tunic of the tuber is the base of the first aerial leaf.

Tribe Allieae—*Brodiaea hyacintha* var. *lactea*.

The seed, 4 mm. long, is covered by a strong black testa.

Germination is Type B. The cotyledon consists chiefly of a tubular sheath (4·5 mm.), with a short inclined stalk (1 mm. long) leading to the suctorial tip. The strong, persistent primary root is proportionately very long (20 mm. in the youngest seedling examined). The plumule is well developed.

Anatomy.—The cotyledon is traversed by a double bundle. The plumular bud contributes to the diarch stele of the primary root. Sargant (120) refers it to the *Allium* type of transition.

Iridaceae.

The seedlings examined offer so many points of similarity that only *Crocus* will be described in detail.

Crocus.

Crocus speciosus var. *albus*.—The seed is small and spherical. Six months elapse before germination (Type B) occurs (fig. 24). Thereafter development is slow. Maw mentions the lengthy time required for germination in the genus but gives no description of the seedling or of the initiation of the corm. The cotyledon stalk is short but the sheath of considerable length. Klebs (87) referred to the absence of root hairs on the primary root of *Crocus*.

The first indication of the development of a corm is the appearance of a small conical lateral outgrowth, pointing downwards and arising at the base of the cotyledon on the side remote from the stalk and seed.

Anatomy of Seedling showing Development of the Corm (fig. 24).—The cotyledon possesses a single vascular strand which is evidently a greatly reduced double bundle. The first leaf is cylindrical and has four strands towards the base but three near the tip. The second leaf has five vascular strands, and shows the two invaginations responsible for the form of the adult leaf.

The cotyledon strand joins the plumular traces before fusion of the cotyledon base with the axis is complete ; the base of the first internode at this level is swollen. The mass of vascular tissue is irregularly disposed towards the centre

of the axis, but the cormic development, though chiefly originating in the hypocotyl, is lateral. The embryonic corm has no vascular tissue except that shared by the hypocotyl, the strands on the side nearest the corm being derived from the plumule. The primary root is in an almost direct vertical line with the cotyledon strand. It is tetrarch and, at this stage of development, contractile. The lower part of the

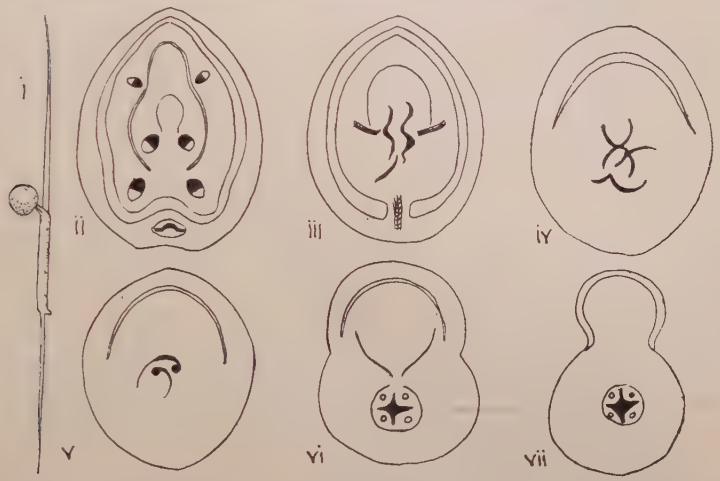

Fig. 24.—*Crocus speciosus.* i. Seedling in which the cormic development has commenced ($\times \frac{2}{3}$). ii–vii. Transverse sections of the seedling figured. ii. Cotyledon sheath enclosing the bases of the first and second leaves. iii. Upper limit of hypocotyl. vi. Base of hypocotyl and diversion of strands into the lateral swelling which is the origin of the corm.

cormic body lies between the intact root stele and the root cortex, which thus acts as part of its first protective layer.

The arrangement of the vascular skeleton to ensure that the corm is in communication directly with the plumular traces and less directly with the primary root recalls that in *Erythronium* when dropper formation is in progress (13, 115).

The cotyledon of *Crocus vernus* has a double bundle, and the primary root is diarch. *C. Skorpili* is similar but has a pentarch root stele.

The development of a corm is clearly exhibited by seedlings of *Melasphaerulea graminea* (fig. 25) and *Lapeyrousia juncea*, approximately one month old. Seedlings of other members of this group were too young when sectioned to show the basal swelling, but the nature of the hypocotyl is similar to that of

the species mentioned ; the base of the first internode is wide and merges imperceptibly into the hypocotyl, which has

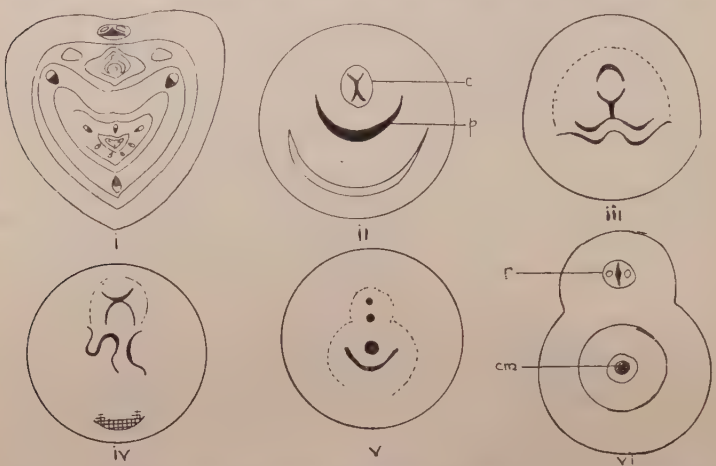

Fig. 25.—*Melasphaerulea graminea*. Transverse sections of young seedling, showing the early stages in corm formation. i. Cotyledon sheath surrounding the three first leaves and buds. ii–v. Hypocotyl. iv. Shows the origin of an adventitious root. vi. Base of hypocotyl, showing root trace (*r*), and the base of the corm (*cm*), which is supplied chiefly by plumular traces.

strong, somewhat scattered strands. The following table of anatomical data shows the main points of resemblance of the species.

Rendle (110) noted the origin of the corm in *Gladiolus illyricus*. Sargant and Arber (124) referred to the anatomy of *Freesia* and *Tigridia Pavonia*.

Aroideae.

To a certain extent germination for genera producing tubers is uniform.

Tribe Arineae—*Arisaema*.

Arisaema Jacquemontii.—The seed, which is spherical, has an average diameter of 1·5 mm.

Germination is Type B. In certain cases elongation of the sheath may lift the seed to the surface. The tip of the cotyledon is cylindrical and lies in a shell of endosperm, surrounded by perisperm. The sheathing base of the coty-

TABLE II.

	Germination.	Vascular Anatomy.		
		Cotyledon.	Primary Root.	First Leaf.
I. Tribe CROCOIDEAE.				
Crocus speciosus var. *albus*	Type B	2 strands	2 poles	3 strands
,, *Skorpili* . .	Type B	2 ,,	5 ,,	4 ,,
,, *vernus* . .	Type B	2 ,,	4 ,,	4 or 6 ,,
Romulea ramiflora .	Type B	1 strand	3 ,,	2, +1 ,,
,, *pulchella* . .	Type B	1 ,,	3 ,,	6 ,,
II. Tribe IRIDOIDEAE.				
Ferraria undulata .	Type C	1 ,,	2 ,,	5 ,,
Tigridia Pavonia . .	Type C	1 ,,	2 ,,	3 ,,
Hexaglottis longifolia .	Type C	1 ,,	2 ,,	6 ,,
III. Tribe IXIOIDEAE.				
Dierama pulcherrima var. *alba* . .	Type B	1 ,,	4 ,,	5 ,,
Gladiolus sp. . .	Type B	1 ,,	3 ,,	4 ,,
,, *gaudavensis* .	Type B	1 ,,	4 ,,	4 ,,
Ixia scariosa . .	Type B	1 ,,	3 ,,	7 ,,
Lapeyrousia juncea .	Type C	1 ,,	4 ,,	5 ,,
Melasphaerulea graminea	Type B	1 ,,	2 ,,	5 ,,
Watsonia sp. . .	Type C	1 ,,	5 ,,	7 ,,

ledon may be 5 mm. in length when the total length of the seedling is only 7 mm. The primary root, which has a strong root cap, is poorly developed. The first leaf is differentiated into sheathing base, slender stalk, and cordate lamina.

Anatomy.—The first leaf had not emerged through the cotyledon sheath at the stages examined. Four strands proceed from the tip of the cotyledon and are increased to five before leaving the seed to proceed through the sheath. A line of weakness in the upper sheath indicates where the slit will occur to free the first leaf. To regard the vascular system of the sheath as a mid-rib and two pairs of lateral strands, as Sargant (120) suggests for *Arum*, is unjustifiable, since certain cotyledons of *Arisaema* have only four strands. At the base one strand is halved and another joins the plumular axis. The other strands gradually form three converging

rays joined by three traces from the plumule. The xylem forms a central plate, flanked by two smaller patches. Lower

Fig. 26.—Seedlings of Iridaceae. i. *Libertia grandiflora* (×2). ii–iii. *Aristea Ecklonii* (×8). iv. *Marica humilis* (×$\frac{3}{2}$). v. *Tigridia Pavonia* (×8). vi–vii. *Libertia ixioides* (×2). viii. *Ixia scariosa* (×2). ix. *Hexaglottis longifolia* (actual size). x. *Sisyrinchium californicum* (actual size). xi. *Watsonia* sp. (actual size). xii. *Melasphaerulea graminea* (×$\frac{3}{2}$). xiii. *Dierama pulcherrima* (actual size). xiv. *Diplarrhena Moraea* (actual size). xv. *Lapeyrousia juncea* (×2). xvi. *Ferraria undulata* (×$\frac{3}{4}$).

it is surrounded by an endodermis and gives rise to a pentarch stele. A seedling in which there are four cotyledon strands, uniting with four plumular traces, has a triarch root stele which lower becomes diarch.

The ray formation of the vascular tissue in the hypocotyl possibly indicates preparation for tuberisation which is otherwise not apparent at the stage examined.

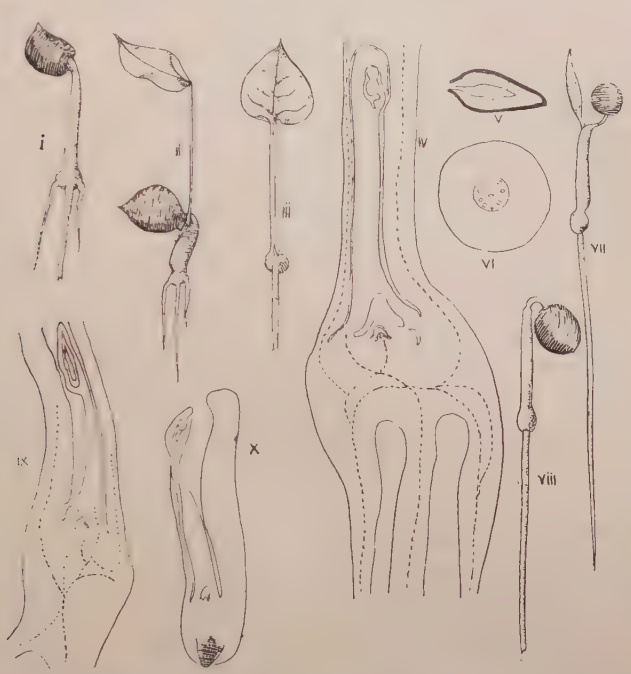

Fig. 27.—i. *Arisaema triphyllum*: young seedling, showing the beginning of corm formation (×2). ii. *Arisaema triphyllum*: emergence of the first leaf (×2). iii. *Arisaema intermedium*: plant six months old with one leaf expanded; the remains of the cotyledon adhere to the apex of tuber, the periderm of which is pigmented; the primary root is contractile (×$\frac{3}{2}$). iv. Longitudinal section of seedling of *A. triphyllum* figured in i (×18). v–viii. *Arum italicum*. v. Longitudinal section through the seed, showing the suctorial tip embedded in endosperm (×4). vi. Transverse section of suctorial tip, surrounded by endosperm, in the neighbourhood of the micropyle (×20). vii–viii. Two seedlings in which tuber formation has begun (actual size). ix–x. *Arisaema triphyllum*. ix. Longitudinal section of seedling, showing tuber formation (×10). x. Longitudinal section of seedling of the same age in which the first leaf has ruptured the cotyledon sheath, but food storage has not proceeded far (×10).

Arisaema concinnum.—The seedlings show marked tuberisation of the hypocotyl. Germination and general anatomy differed in no essential from those of *A. Jacquemontii*. The cotyledon strands do not join the plumular traces in the hypocotyl, but proceed independently through the swollen axis.

The primary root persists for several months. Adventitious roots arise at the base and at the middle of the tuber.

Arisaema consanguineum repeats in its seedling structure the external morphology and anatomy of *A. Jacquemontii*.

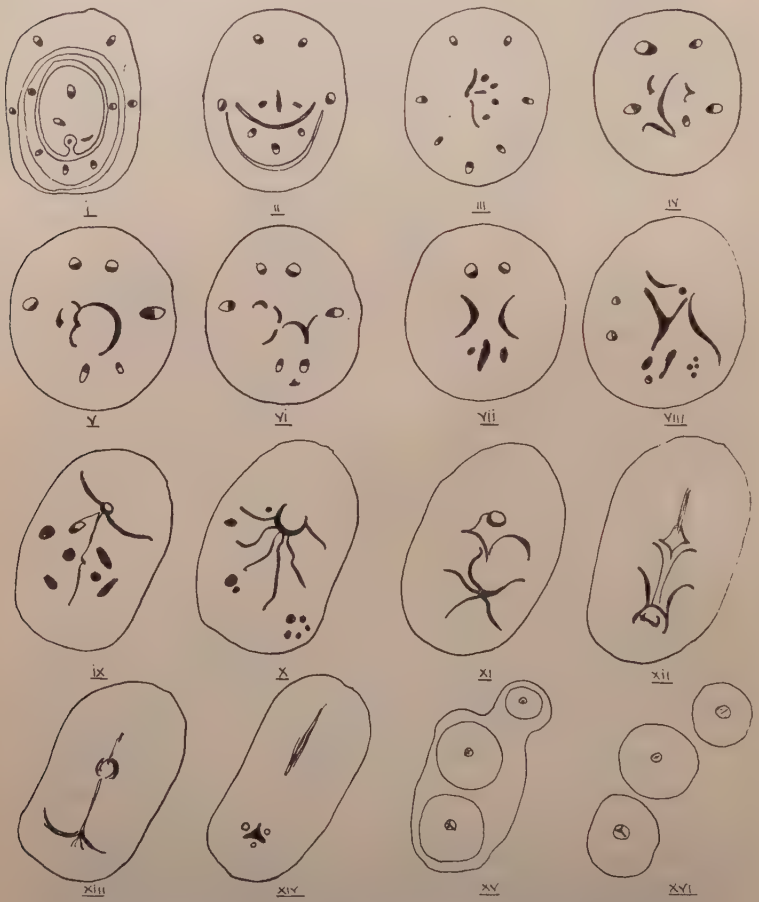

Fig. 28.—*Arisaema triphyllum*. Transverse sections of young seedling with a tuberous hypocotyl. i. Cotyledon sheath enclosing the bases of the young leaves. iii. Upper limit of the hypocotyl. iv–xiv. Hypocotyl. xv. Base of hypocotyl. xvi. Primary root (triarch) and two adventitious roots.

Arisaema triphyllum.—As many as nine strands may be found in the bulky tip of the cotyledon, but they reduce to four in the sheath, and run parallel to the plumular traces for some distance through the tuberous hypocotyl (figs. 27, iv ;

28). The plumular traces form a crescent which, lower, breaks down. No definite hypocotylar stele exists at any level and the vascular strands supply two strong adventitious roots in addition to the triarch primary root. A diarch adventitious root is supplied principally from first leaf traces. The steles of the primary and first two adventitious roots arise about the level of the tuber's maximum diameter and proceed through a ground mass of starchy parenchyma, each maintaining its own identity.

MacDougal (99) described the germination and Rennert (111) in great detail the morphology of the germination of this species, but not to the same extent the anatomy. The former writer emphasised the delayed development of the plumule and the enlargement of the corm simultaneous with the production of the first leaf. Etiolation experiments showed that germination without development of the plumule had occurred. A central and two pairs of lateral strands were found in the cotyledon, and triarchy in the primary root.

Arisaema intermedium (fig. 27, iii).—Sections were made through the tuber of a seedling six months old. The only trace of the cotyledon was a scar where the upper portions had been cut off by periderm. The outer protective layer, doubtless cotyledonary, consisted of periderm six cells deep. The covering of the tuber is spotted with a red pigment. The food reserve is starch. Five leaves (apparently scale leaves) form a conical apex of the tuber in which a massive stele is surrounded by five or six smaller root steles. The primary root is contractile. Roots may arise towards the top of the tuber.

Sargant (120) recorded seven to nine cotyledonary bundles and a triarch or tetrarch root in the seedling of *A. speciosum*.

Arum.

Arum hygrophilum in germination and anatomy resembles the seedling of *Arisaema*, but the seed and seedling are almost twice as large. Six strands are found in the cotyledon. The hypocotyl exhibits the scattered arrangement seen in other tuberous seedlings, though the strands are weak. The primary root, which is remarkably lengthy and strong, is pentarch; it later becomes contractile.

Arum italicum is similar. The cotyledon, however, has seven strands towards the upper part of the sheath, although there are only six at the base of the sheath. (Gatin (57) recorded five strands in the sheath.)

For the purpose of comparison within the family, the seedlings of two further genera, which have not a tuberous habit, will now be described.

Tribe PHILODENDREAE—*Richardia Elliottiana.*

The adult plant is rhizomatous.

Gatin described the seed and poorly differentiated embryo of *R. aethiopica* Kunth but not the germination.

The seed of *R. Elliottiana* (5 or 6 mm. long), which contains starchy endosperm, has a ribbed testa and is three or four times as large as that of *Arisaema*. A copious production of adventitious roots occurs in the young seedling

Anatomy (fig. 29).—The cotyledon tip is cylindrical and occupies half the diameter of the seed. Towards the distal end of the tip three arms of vascular tissue proceed radially for a short distance from the centre. Nearer the micropyle the arrangement is a hollow cylinder with two gaps, the xylem forming the inner, and the phloem the outer ring. A double bundle and four pairs of lateral strands occur in the sheath of the cotyledon.

The first leaf has a mid-rib and three pairs of lateral strands which, with the primordia of the second leaf, contribute four traces to the hypocotyl at a level where the strands of the cotyledon are fusing in adjacent pairs. The mid-rib alone pursues an unaltered course. Fusion between cotyledon and plumular strands does not occur in the hypocotyl. The stele of the primary root is principally derived from cotyledon strands, the central double bundle being responsible for one root pole. The root, throughout its length, is hexarch. In view of the proportions of seed, cotyledon, and plumular bud, the development of the root is relatively weak.

Tribe ORONTIEAE—*Anthurium Scherzerianum.*

The plant belongs to a tribe containing many epiphytic forms. The ovoid seed (2·5 mm. long) is endospermic and has

a polished, yellow-white testa which at germination becomes green. Gatin (57) described the very small conical embryo of this and other species. The plumular bud, which is weakly differentiated, is protected by two imbricate folds of tissue edging the cotyledon slit. A single median procambial strand passes through the embryo.

The bright red berries were placed on a coarse mixture of coco-nut fibre and dead leaves and left in the tropical germinating house. Each day a berry was broken, three or four

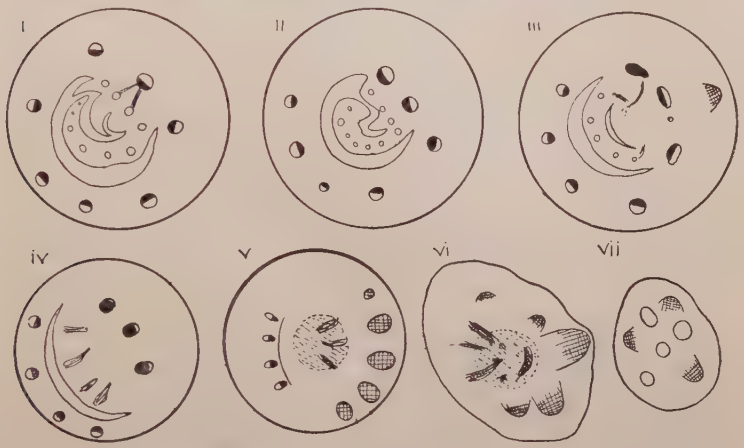

Fig. 29.—*Richardia Elliottiana*. Transverse sections of seedling a few days old. i. Base of the cotyledon sheath: the node is oblique. iii–v. Hypocotyl. vi. Lower limit of hypocotyl; note the ring of strong adventitious root initials.

seeds being obtained from each. The early stages of germination may take place within the berry; this also occurs in nature. Germination is Type B (fig. 30). The primary root of a seedling twelve hours old is a short, blunt cone, emerging from the seed through a toothed aperture. A collar of long root hairs appears immediately on germination. The short, wide sheathing base of the cotyledon, then visible, is photosynthetic. Five days later the first leaf breaks through the cotyledon sheath, which has then attained its maximum length (2 mm.). Growth in the root and shoot now proceeds rapidly. The first leaf is differentiated into a short basal sheath, a narrow petiole (1 cm. long), and an obovate-lanceolate limb smaller than that of succeeding leaves but with the same reticulate venation. Gatin (57) figured this stage of

germination, but anatomical data and his detailed observations on the development were evidently not available for publication. The second leaf, which is diametrically opposite to the first, emerges from the sheathing base of the latter. The first internode, which at this stage is 1–2 mm. in length, may be oblique to the primary root, or horizontal. Strong buttressing

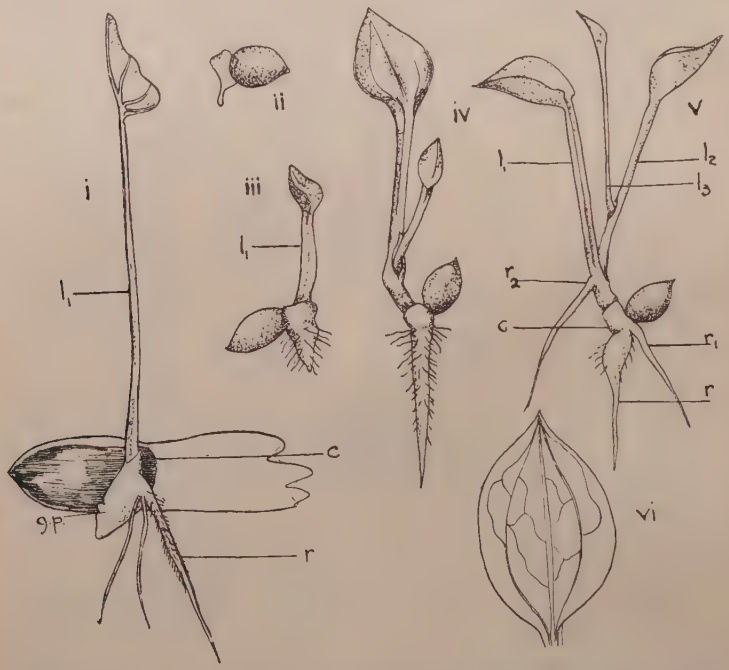

Fig. 30.—i. *Testudinaria sylvatica*: seedling with first leaf expanded, showing tuber formation; the cotyledon sheath surrounds the apex of the tuber ($\times \frac{3}{2}$). ii–vi. *Anthurium Scherzerianum*. ii–iii. Seedling two days and seven days old ($\times 2$). iv–v. Later stages in development ($\times 2$). vi. Venation of first leaf ($\times 4$).

c = cotyledon; l_1, l_2, l_3 = first, second, and third leaves; $g.p$ = growing-point of tuber; r = primary root; r_1, r_2 = first and second adventitious roots.

roots arise from the base of the first and second internodes obviously in relation to the growing leaves. A shorter internode separates the second and third leaves.

Anatomy.—The mid-rib and two lateral traces of the lamina of the first leaf descend the petiole, and a fourth weak trace from the plumular bud enters the lowest internode with them. A single vascular strand proceeds from the tip to the base of

the cotyledon and becomes involved in the rapid transition. The primary root is diarch. An exodermis of large regular cells occurs in the primary and the early cauline roots, in which the stele is triarch.

Literature on the Seedlings of Aroids.

The germination of *Anthurium*, though by no means typical, represents the family in Lubbock's work (97). Klebs (87) places two species of *Arum* in Type I.

The first thorough investigation of general morphology, detailed anatomy, and developmental stages of an Aroid seedling appears to have been made by Scott and Sargant (133) on *Arum maculatum*, in which growth is extraordinarily slow (the first ovate leaf appearing only in the third year). In structure the seedling resembles the species of *Arum* described. The tuber is regarded as belonging to the stem, since it shows no root structure, and the formation of a vascular girdle at the nodes, characteristic of the adult, is observed in the youngest seedlings. No part of the hypocotyl shows the character of a true stem. There are five strands in the cotyledon, while the primary root has a tetrarch, and lower a triarch, stele. Sargant (120) stated that the peculiar habit of *Arum* has modified the vascular system of the cotyledon, and suggested that *Anthurium Bakerianum*, which has a double bundle in the cotyledon, has a transition more primitive than *Arum*, the former being derived from *Anemarrhena* through so-called transitional Liliaceous forms. The primitiveness of the *Anthurium* cotyledonary anatomy, compared with *Arum*, is, in the opinion of the present writer, debatable.

Campbell (21–24) published a series of studies in which the embryonic and post-seminal development of certain genera is taken to indicate primitiveness; for example, the lateral development of the primary root of *Lysichitum camtschatcense* is thought to suggest *Isoetes*. Preponderance of cotyledon and very slight differentiation of primary root in the embryo were characteristic also of *Aglaonema* and *Spathicarpa*. *Nephthytis liberica* had an embryo 1 cm. long (the greater part of the mature seed) of which root and stem were "relatively poorly developed." Of *Anthurium violaceum* Campbell noted that, "like other low monocotyledons, the embryo is

far advanced when the seed is ripe." The inference regarding primitiveness and embryonic differentiation might be questioned.

MacDougal (99) noted that *Arisaema Dracontium* was saprophytic in its first season, while its corm develops before the plumule emerges. Rennert (111) extended the observations and made a comparison of the morphology and physiology of *A. Dracontium* and *A. triphyllum*. Of the seedlings examined only 10 per cent. had functional plumules, and these tended to degenerate. It was concluded that *A. Dracontium* is losing its power of producing a normal assimilatory plumule, though its highly organised hypocotylar vascular system, of little service to a seedling without a plumule, is retained.

Chrysler (32) believed that the peculiar habit of sprouting may have modified the vascular tissue in *Arum italicum*, which he termed a " highly organised " seedling with " no suggestion of primitiveness."

From a study of the seedlings, A. W. Hill (1906) concluded that *Arum* and *Arisaema* are allied to the Piperaceae and not far removed from a Dicotylous ancestry; but *Anthurium*, due to xerophily, shows analogies to a more ancient group of Lilies in which the simplest forms possess a single bundle and the most ancient a double bundle in the cotyledon. The Aroids he considers a more primitive and less highly specialised group than the Liliaceae.

Gatin (57) concentrated on the morphology of the ripe embryo and the initial stages of germination. The following genera were dealt with: *Pothos*, *Acorus*, *Spathiphyllum*, *Aglaonema*, *Nephthytis*, *Dieffenbachia*, *Zantedeschia*, *Caladium*, eight species of *Anthurium* and four of *Arum*. Germination of all these genera was not observed.

Boodle and Hill (14) have recently described the seedling of *Typhonodorum Lindleyanum*, a viviparous swamp plant. The main portion of the young embryo consists of a dense corm-like body on the upper side of which lies the plumule, while from the lower side a peg-like, spongy haustorium develops. The corm is regarded as a specialised portion of the cotyledon or a lateral hypocotyledonary outgrowth. In addition to its food-storing capacity, the corm-like body acts as a float. *Cryptocoryne ciliata* Fisch., described in 1847 by Griffith (63) under the name of the *Ambrosina ciliata* Roxb.,

affords a comparable case. The young plant, when liberated into the water, consists of an upper plumular part, very short stem and root rudiments, and a lower part which is the haustorial cotyledon. Unlike the haustorium of *Typhonodorum*, the latter organ soon breaks away from the rest of the plant. The first three to six leaves are all petiole. After rooting, succeeding leaves develop a lanceolate or ovate lamina, and later the mature form. Griffith remarks of *Cryptocoryne* that the highly developed plumule obviates the necessity for the cotyledon.

Dioscoreaceae.

Tamus communis.

Microtome sections were not made, Queva (107) having fully described the anatomy.

The embryo is small compared with the seed, which is spherical and 3–4 mm. in diameter. Germination is Type B. The cotyledon sheath is short and arches up, giving a low upper sheath. There is no perceptible stalk region. The suctorial tip, after germination, fills half the seed, and may be cylindrical or club-shaped. One vascular strand proceeds through the cotyledon sheath and very short stalk. It ramifies in the tip, producing six or seven peripheral traces. The primary root, which is triarch and early reinforced by cauline roots, is inserted on the anastomosing fibro-vascular mass that results in the hypocotyl from the union of plumular and cotyledon strands. The hypocotyl is exceedingly short. The tuber is initially a lateral outgrowth on the " dorsal face " of the hypocotyl—that is, it is produced on the side remote from the seed. It receives the primary strands inserted on the hypocotylar vascular system, and later elongates downwards, due to the activity of a positively geotropic growing-point. Cambium forms in two zones : the inner produces fundamental tissue and secondary vascular tissue ; the outer cambium lays down cork. At this later stage the tuber results from hypertrophy localised in the hypocotylar axis, but also involving the two first internodes. According to Queva it is anatomically a stem, morphologically it has the exterior of a root, and physiologically is food-storing tissue.

Testudinaria Elephantipes.

The seed is flattened and winged. Its length is 6–7 mm. (15 mm. including the wing). In germination and seedling morphology it resembles *Tamus communis*. Tuber formation had begun in the youngest plant examined (seven weeks old), when the lamina of the first leaf had partially expanded. There are curious hairs on the petiole of the latter. *T. sylvatica* exhibits the same features.

Queva reduces the tubers of Dioscoreaceae to four types :—

(*a*) The *Tamus* type, the origin of which has been referred to, is traversed by secondary vascular tissue save for a few small hypocotylar strands.

(*b*) The *Helmia* type arises by hypertrophy of the base of the primary stem and the hypocotylar axis. The tubers are annual and the vascular system primary. Morphologically they are more advanced than those of group (*a*).

(*c*) The type illustrated by *Dioscorea Kita*, in which the tuber arises from the hypertrophy of one side of the hypocotylar axis.

(*d*) Tubers which are "rhizomatous" produced from an axillary bud of the second leaf.

Schlickum (127) has described the anatomy of *Dioscorea bulbifera* L. and Dale (37) the origin of the aerial tuber in *D. sativa* L., remarking that it was produced by the swelling of the first epicotyledonary internode of the seedling.

Regeneration experiments by means of leaf cuttings in species of *Dioscorea* [1] indicate that the tuber which forms shortly after the leaf has rooted is not wholly hypocotylar in origin.

Summary.

The corm or tuber originates in various ways as the following examples show :—

(i) In *Colchicum autumnale* L. it arises as a lateral swelling of the hypocotyl. The upper part of the root acts, with the base of the cotyledon, as a protective covering. The descent of the corm in the soil is peculiar.

(ii) *Gloriosa*, another Liliaceous genus, produces its tuber by the swelling of the primary stem, from a level above the second node, to the base of the third internode, sheathed by the bases of the first and second foliage leaves (see p. 135).

(iii) The cormic development of *Crocus*, *Lapeyrousia*, and *Melasphaerulea* is lateral, arising from and below the base of the

[1] Trans. Bot. Soc. Edin., xxx, pt. iv (1931), p. 282.

first node. Its origin is therefore hypocotylar. It is protected by the epidermis of the sheathing base of the cotyledon and the hypocotyl. The epidermis of the upper part of the root is displaced outwards and sheathes the lower part of the young corm.

(iv) Rendle (110) states that the corm of *Gladiolus illyricus* arises during the first vegetative season by thickening of the internode above the insertion of the first leaf. It is at first surrounded by the thin sheath of the cotyledon, which soon disappears. The sheath of the succeeding foliage leaf forms a dry membrane round the corm.

(v) The Aroids form tubers by the storage of food reserve, usually starch, in the hypocotyl. The vascular supply of the tuber in the first instance is the original hypocotylar traces of the seedling. The first internode or the upper portion of the radicle is not involved in tuberisation.

(vi) Tubers of the Dioscoreaceae may originate from hypertrophy of the hypocotyl, and the two lower internodes (*Tamus*, and some *Dioscoreae*) from hypertrophy of only one side of the hypocotyl (*Dioscorea Kita*), or from an axillary bud of the second leaf. (Queva.)

The seed in the Aroids at maturity may or may not be albuminous (57). Where the development of the plumule is late, the endosperm is directly responsible for the increase in volume of the corm or tuber. Data are not available for the size of seeds of plants mentioned in literature, but, in the genera actually examined, it seems that large-seeded types, such as *Arisaema* and *Arum*, tend (in contrast to the small-seeded rhizomatous *Anthurium*) to have numerous cotyledonary strands.

Germination is hypogeal. Of thirteen genera of Iridaceae only four had ligulate cotyledons; *Merendera Bulbocodium* Ram., *Colchicum autumnale* L., and *Gloriosa* (Liliaceae) furnish additional examples. The Aroids are without exception non-ligulate, although the cotyledon of *Anthurium* tends to form a short upper sheath.

Tuberisation is not foreshadowed in the embryo. Campbell's and Gatin's researches on the embryo of the Aroids reveal instances of embryos with very poorly defined tissues. Gatin (57) pointed out that there is a gradation in the differentiation of the embryo, but, since no facts were given regarding the germination of *Caladium* and *Spathiphyllum*, the embryos of which are poorly differentiated, a comparison correlating embryonic structure with the tuberisation of the seedling cannot be made. In MacDougal's study of *Arisaema*

Dracontium (99) delayed germination is associated with early tuberisation, an observation confirmed by the germination of *Crocus*. In the Aroideae the plumular development of *Arum maculatum* is most backward, three seasons elapsing before the production of an aerial leaf (133). Several species of *Arisaema* possess a corm before the first leaf is set free from the cotyledon sheath, and in general only one leaf functions during the first season. The corm or tuber then apparently enlarges at the expense of the other organs. The early production of leaves in *Anthurium*, which does not form a tuber, offers a marked contrast to the development in *Arum* and *Arisaema*. The Dioscoreaceae examined, like the tuberous Aroids, have a solitary leaf during the first year, but seedlings of the Iridaceae have a normal rate of plumular development. Two of the three exalbuminous seeds described by Gatin produce embryos with two plumular buds—a phenomenon to be connected possibly with the undifferentiated state of the embryos.

Nature of the First Leaf.—In *Crocus*, *Romulea* (Iridaceae), *Nephthytis*, *Cryptocoryne* (Aroideae), and *Dioscorea repanda* the first leaf is a sheath. In *Anthurium* it has a limb of the normal form, but reduced in size. *Arisaema*, the remainder of Aroideae, and Dioscoreaceae examined exhibit a first foliage leaf which is differentiated into sheath, long petiole, and cordate, net-veined lamina. Though the plumular development is poor regarding the number of leaves, the single leaf above ground is efficient.

Anatomy of the Cotyledon.—The Liliaceae have a double bundle in the cotyledon. In Iridaceae there may be a single or double bundle (Sargant records a mid-rib and two lateral strands in *Freesia* sp.). In the Dioscoreaceae for which information is available there is one, or a mid-rib and two lateral strands (*Helmia hirsuta*). Larger numbers of strands are found in the Aroids, in which the number may be variable in a species. *Richardia* has a mid-rib (a double bundle) and eight lateral strands, *Arum* six or seven strands, and *Arisaema* four or five, while *Anthurium* is exceptional in having only one strand.

Hypocotylar anatomy is on a similar plan for all. The vascular strands, usually numerous, are scattered but freely anastomose, an arrangement in no way resembling the typical root, but in the axial vascular system unlike a stem. Its

internal morphology seems to be suitable for an organ which in the course of development increases in girth. Yet the arrangement is found in *Richardia*, which does not produce a tuber.

The anatomy of the primary root offers no peculiarity. Diarchy, triarchy, and tetrarchy are common. The root of *Arum*, which has seven cotyledon strands, is pentarch. *Richardia Elliottiana* has a hexarch stele in the primary root. (This species had the most numerous cotyledon strands.) There exists between the number of cotyledon strands and number of poles in the root a relation made more obvious by the two seedlings of *Arisaema triphyllum*, in which the root poles increase with the number of cotyledon strands. The root system of the group suggests a compromise between that of bulbous and of rhizomatous seedlings, for the primary root becomes contractile as in the former group but is early reinforced by numerous cauline roots. In a seedling two months old it is difficult to determine which is the primary root, for at least one other contractile root is equally developed, and three or four purely nutritive roots may in addition be present. While in the majority of seedlings the primary root is lengthy, it may be poorly developed in the Aroideae and Dioscoreaceae. In certain species of *Arum* it persists for a year.

C.—Rhizomatous Plants.

Liliaceae.

Tribe Asphodelieae—*Pasithea coerulea*.

The seed is 3 mm. long and is roughly pyramidal in shape. Germination is Type B. Two vascular strands proceed through the entire length of the cotyledon, which consists of a broad, fleshy, sheathing base, a short, thick stalk, and a barrel-shaped suctorial tip. Development is rapid and involves almost equal rate of growth of root and shoot. Three leaves and the primordia of the fourth are differentiated in a seedling three days old. Internodes are short. The plumular bud is carried 1 mm. or so below the surface. The first leaf, which is linear, has six parallel strands. The levels where the cotyledon strands enter the axis are 100 μ apart, due to the obliquity of the nodes. The xylem

assumes a radial arrangement immediately the second strand fuses with the axial strands. At a level 60 μ lower the stele is completely sheathed by an endodermis. The strong, persistent primary root is covered with root hairs. In young seedlings a collar of three or four hypodermal layers occurs at the upper limit of the primary root, which has a compact stele, with well-developed phloem, and a wide endodermis.

Anatomy of Transition.—The two outer pairs of first leaf traces are joined by one cotyledon strand. A ring of five xylem strands, associated with phloem, results. The strand formed from the two main traces of the first leaf enters the stele at the same level as the second cotyledon strand. Further re-arrangement gives a pentarch root stele.

Arthropodium cirrhatum.

The seed resembles that of *Pasithea*. Germination is epigeal. Two strands proceed from the tip to the base of the cotyledon, the lower limit of which is not obvious, for it passes without change in width into a cylindrical region free from root hairs, approximately 6 mm. long, which may be regarded as hypocotyl although its stele has root symmetry. In the hypocotyl the outer epidermal wall is heavily cutinised. Where root hairs arise, an abrupt diminution in width takes place. The root stele in the four seedlings examined is triarch. The plumule is poorly defined. Sargant (120) refers the transition to the *Allium* type, and finds the root stele diarch.

Chlorophytum Sternbergianum.

The seed is similar to that of *Pasithea*.

Germination is Type C (fig. 31). The long thread-like stalk which connects the sucker to the short ligule may be at germination only 2 mm. long, but at the end of a week is 8 or 9 mm. long. The sheathing base and the ligule are approximately the same length. The first leaf, which is linear-lanceolate, appears above ground in a few days. The primary root in a day-old plant is four-fifths of the seedling's total length. A cylindrical region free from root hairs extends for 6 mm. below the base of the cotyledon sheath, and, though apparently hypocotylar, has a typical root stele. Its lower limit is marked at the level of the seed in the soil by an abrupt

FIG. 31.—*Chlorophytum Sternbergianum.* i, ii, iv, vi. Developmental stages from one day to six weeks old ($\times \frac{1}{3}$). iii. Longitudinal section of seedling figured in ii to show the lengthy hypocotyl ($\times 8$). v. Longitudinal section of seedling in the neighbourhood of the plumular bud, showing the course of the cotyledon strand ($\times 6$). vii. Transverse section of primary root in the swollen water-storing region ($\times 100$). viii. Stele figured in vii ($\times 200$). ix. Transverse section of hypocotyl immediately above the upper limit of the primary root ($\times 300$). x. Transverse section of adventitious root in a region which is not specialised for water storage; the hypodermis is heavily cutinised ($\times 100$).

increase in width. The root (8 mm. long) is densely covered with root hairs, and in older plants may be longer than the shoot. A month-old seedling has three rootlets but no adventitious roots, but two months later there are three cauline roots (each with long branches). At this stage many roots show marked local swelling (in certain instances the greater part of the organ being affected), entirely due to increase in size of individual cortical cells. The cortical zone is three or four times as wide as in the unswollen part, and the stele almost double its original diameter (fig. 31). Increase in the number of protoxylem poles does not occur, but the xylem, which formed a compact ring, disintegrates, large-celled parenchyma alternating with metaxylem and forming a medulla. The function of the cortex is water storage ; starch is absent.

Anatomy of One-week-old Seedling.—A double bundle proceeds through the tip and stalk of the cotyledon and ascends through 0·8 mm. The greater part of the trace then sharply turns and descends, and a weak upward trace (0·35 mm. long) continues higher in the ligule. The first leaf has a mid-rib and two pairs of lateral strands. The inner pair absorb the traces from the plumular bud. The cotyledon downward trace passes to the centre and, incorporating first the outer laterals, fuses with the inner laterals. The phloem of the inner laterals moves peripherally towards that of mid-rib to give one phloem patch, and partly in opposite direction towards the cotyledon strand to give two patches. The xylem does not move but remains in a compact triangular plate, the cotyledon and outer laterals of first leaf together contributing to one xylem pole. The change from stem structure to typical triarch root stele occurs within 50 μ. An endodermal sheath arises 1 mm. below the transition. A seedling with a diarch root was found. In the region free from root hairs the epidermal cells are very small, square, and regularly arranged, with marked cutinisation on the outer tangential wall. Exodermal cells are larger and square-shaped, with outer tangential and radial walls thickened. Cortical cells are very large and isodiametric. As the primary root ages, it thickens and the stele becomes tetrarch or pentarch. The xylem may be centralised or in a medullated ring. Lateral roots and cauline roots have five to eight xylem poles.

Trichopetalum stellatum.

The seed is small, 1 mm. long.

Germination is epigeal. The plumular bud is weakly differentiated. Two strands in contact proceed through the cotyledon. The primary root is triarch and has a wide and succulent cortex.

Tribe HEMEROCALLEAE—*Hemerocallis spicata.*

The seed is roughly spherical. It is covered by a smooth black testa and is large and heavy (6 mm. × 5 mm.).

Germination is Type B (fig. 32). The primary root pushes off a circular lid on germination. The cotyledon consists of a large, club-shaped tip and strong sheath, at the base of which a collar of parenchyma occurs. The robust nature of the seedling is noteworthy. The strong primary root is densely covered by root hairs but devoid of lateral roots. Three leaves and a strong bud develop before the end of the first week. Growth proceeds equally for root and shoot although the length of the primary root in the young seedling may be twice as long as the aerial part of the seedling.

Anatomy.—Four strands follow a parallel course from the tip of the cotyledon to the base of the sheath, at which level they are inserted one by one on the plumular traces. In the cotyledon of one seedling six strands were found. The first and second leaves have ten vascular strands; the ring of the vascular traces at the lower limit of the axis is accordingly strong. The primary root is pentarch and has a wide water-storing cortex and an exodermis of very large, squarish cells. In the seedling with six cotyledonary strands the root stele was hexarch.

Hemerocallis nana.

This differed anatomically from *H. spicata.* The cotyledon has five strands in the tip and sheath. The first leaf has a mid-rib with three pairs of laterals, and subsidiary traces between each pair, while the root is heptarch.

Hemerocallis Forrestii.

This species differs from the two described in its seed, which is more nearly spherical and slightly larger (6·5 mm. × 6·0 mm.),

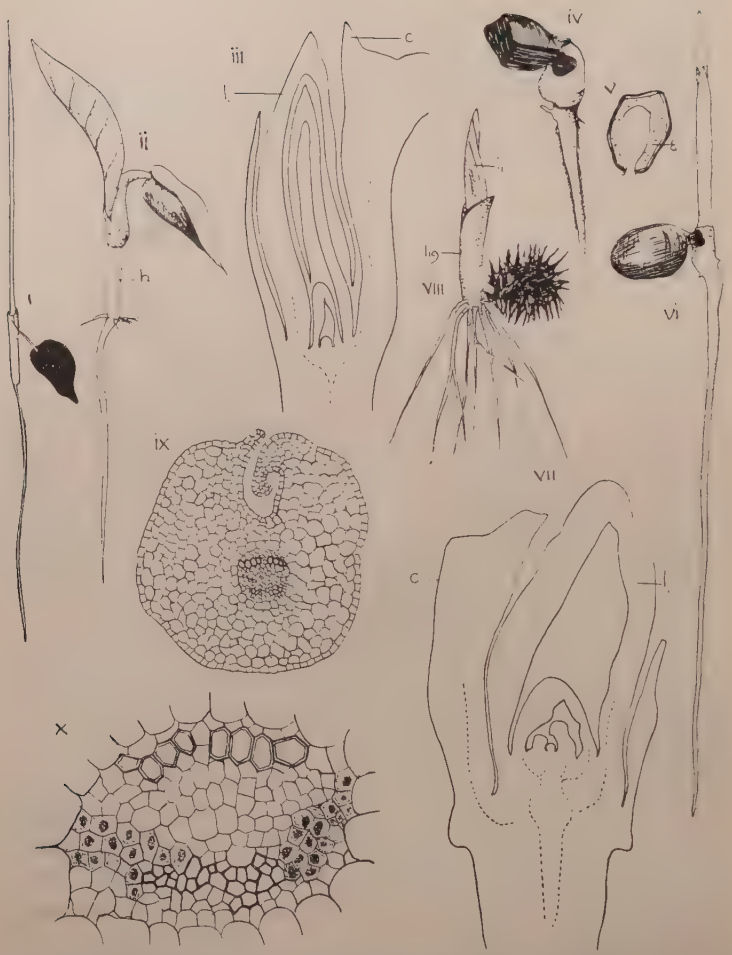

Fig. 32.—i. Seedling of *Phormium tenax* (× ⅔). ii–iii. *Funkia ovata*. ii. Seedling of which the first leaf has emerged (× 5). iii. Longitudinal section of younger seedling (× 15). iv–vii. *Hemerocallis spicata*. iv. Seedling three or four days old (× 3). v. Tip of cotyledon embedded in endosperm (× 3). vi. Seedling, showing emergence of second leaf (× 3). vii. Longitudinal section of seedling one week old (× 15). viii. Seedling of *Wachendorfia thyrsiflora* (× 3). ix. Transverse section of lamina of cotyledon of *Anigozanthos Manglesii* (× 40). x. Cotyledon strand of *A. Manglesii* (× 300).

c = cotyledon; *e* = endosperm; *lig* = ligule; l_1 = first leaf; *h* = hypocotyl.

and also in its seedling anatomy. There may be four, five, or seven strands in the tip of the cotyledon, and seven in the sheathing base. In one seedling the stalk region between sheath and tip, which is almost non-existent, is hollow like an inrolled leaf. The primary root is hexarch. The first leaf has ten strands.

Phormium tenax.

The seed is endospermic. It is flattened, 7 mm. long, omitting the membraneous edge of the testa, which is thin and black (fig. 32).

Germination is Type B. The seedling is long and thin. A filamentous stalk (2–3 mm. long) connects the suctorial tip to the long sheathing base. The primary root, which is pentarch, is persistent and fairly well developed. (It is 10 mm. long in a seedling whose shoot portion is 35 mm. high.) The first leaf has a mid-rib and three pairs of lateral strands. Two strands proceed from the tip to the base of the cotyledon.

Funkia ovata Spreng.

The seed (3–5 mm. long) is three sided. The black testa forms a membraneous wing at the end distal from the micropyle. The embryo is spindle-shaped, 1–2 mm. in length.

Germination is Type B (fig. 32). The cotyledon has a tubular sheathing base, short stalk, and cylindrical sucker. The plumular development is strong; a week-old plant has three leaves differentiated, the oldest having pierced the apex of the cotyledon sheath. The primary root is then 1 cm. in length. It is persistent and at first is of equal, then for a period of greater, length than the aerial portion of the seedling. The maximum length of the hypocotyl is 3–4 mm. Nineteen days after germination the second leaf has expanded. The appearance of lateral and adventitious roots coincides with the emergence of the second and succeeding leaves.

Anatomy.—A double bundle proceeds through the entire length of the cotyledon, enters the axis at a gentle angle some distance below the first node, and for a short distance in the hypocotyl remains independent. The lamina of the first and succeeding leaves is cordate. At the base of the first

leaf the two lateral strands on each side of the mid-rib unite with one another, reducing the leaf traces to three, then to two strands, which are joined by the cotyledonary strand at the base of the axis. The hypocotylar stele is enclosed by a thin-walled endodermis and consists of a band of xylem (of plumular and cotyledonary elements) separating two meristematic traces, mostly phloem, chiefly derived from the plumule. The root stele is diarch.

Blandfordia marginata.

The seed is 4 mm. long, covered by a dark brown testa, and spindle-shaped. Germination is epigeal. The seedling is very slender. Root and cotyledon are equally developed.

Anatomy.—The cotyledon possesses a single collateral strand in which only four xylem elements occur. In the hypocotyl, which is 2–3 mm. long, the xylem is placed in a band across the stele as in *Funkia*; there is an enclosing endodermal sheath. Four small groups of xylem (with one or two elements in each) are peripherally arranged in the weak root stele.

Tribe Medeoleae—*Paris polyphylla.*

The early life-history of this plant has been elsewhere described (15). The seedling (fig. 33), arising from a small undifferentiated embryo, has a highly specialised cotyledon consisting of a sheathing base, which becomes a food-storage organ, a thin cylindrical "petiole," and a broad, cordate, photosynthetic lamina, reticulately veined like the foliage leaves. Development is extremely slow. The cotyledon traces (a mid-rib and two lateral strands) remain vertical, whereas with growth of the hypocotyl the weak plumular traces become oblique (fig. 33, II*b*, III*b*). The lateral strands of the cotyledon fuse with the axial stele 0·5 mm. below the level where cotyledon, mid-rib, and plumular traces merge. The upper limit of the hypocotyl may be regarded as the level at which the lateral traces join the others, though Sargant would have placed it at the fusion of plumular traces and mid-rib. In the hypocotyl the closed or open rings of xylem are buttressed outside and inside by phloem, the vascular tissue lying in a parenchymatous ground mass (fig. 35). The con-

tractile primary root is triarch, towards the tip diarch, and finally mon-arch (fig. 34). A cauline root is produced during

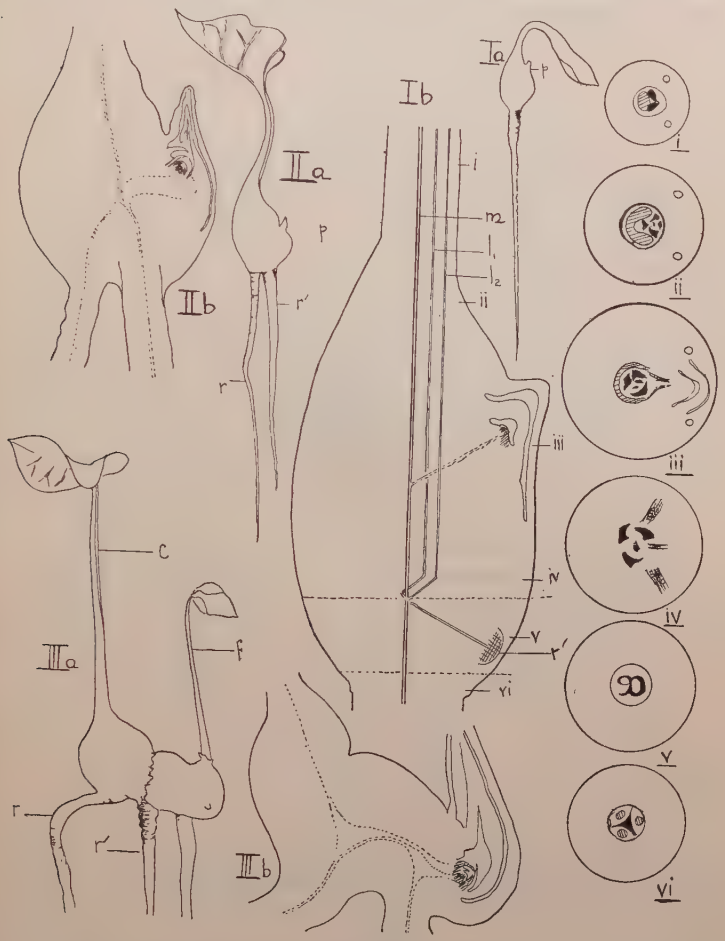

FIG. 33.—*Paris polyphylla*. Ia. Seedling four months old (×3). *b*. Longitudinal (diagrammatic) section of same seedling and transverse sections i–vi at the levels indicated; dotted lines indicate the limits of the hypocotyl. IIa. Seedling six months old (×2). *b*. Longitudinal section of seedling six months old. IIIa. Plant a year old, showing development of monopodial rhizome (actual size). *b*. Longitudinal section of tuber.

c = cotyledon; *f* = first leaf; *m* = mid-rib of cotyledon; *p* = plumular bud; l_1, l_2 = lateral strands of cotyledon; *r* = primary root; *r'* = adventitious root.

the first year. The horizontal traces in a year-old seedling function as the vascular system of a monopodial rhizome (81),

the plumule placed at the end of the first node. At this stage the base of the cotyledon and the hypocotyl comprise one-half of the rhizome, while the cotyledon strand maintains connec-

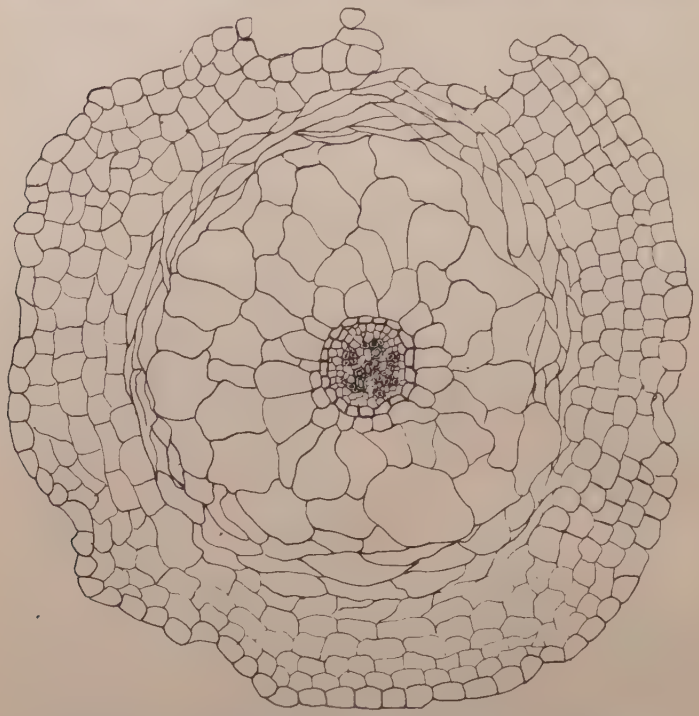

FIG. 34.—*Paris polyphylla.* Transverse section of contractile primary root (× 90).

tion with plumule and primary root by a necessarily indirect course.

Trillium ovatum.

A year elapsed before germination commenced (fig. 36). Subsequent development was slow. Morphologically the seedling closely resembles *Paris*. The cotyledon is for a considerable period the only photosynthetic organ. The lamina, which is somewhat narrower than that of *Paris*, gradually unfolds and detaches its tip from the seed. The plumular bud is sheathed by the cotyledon base, and appears as a small lateral protuberance towards the top of a very

swollen hypocotyl, which merges downwards into a thickened region, covered profusely with root hairs. The first leaf resembles the cotyledon in shape and veining. At first it is bent at the juncture of petiole and lamina, and by degrees straightens. The petiole is long, cylindrical, and narrow;

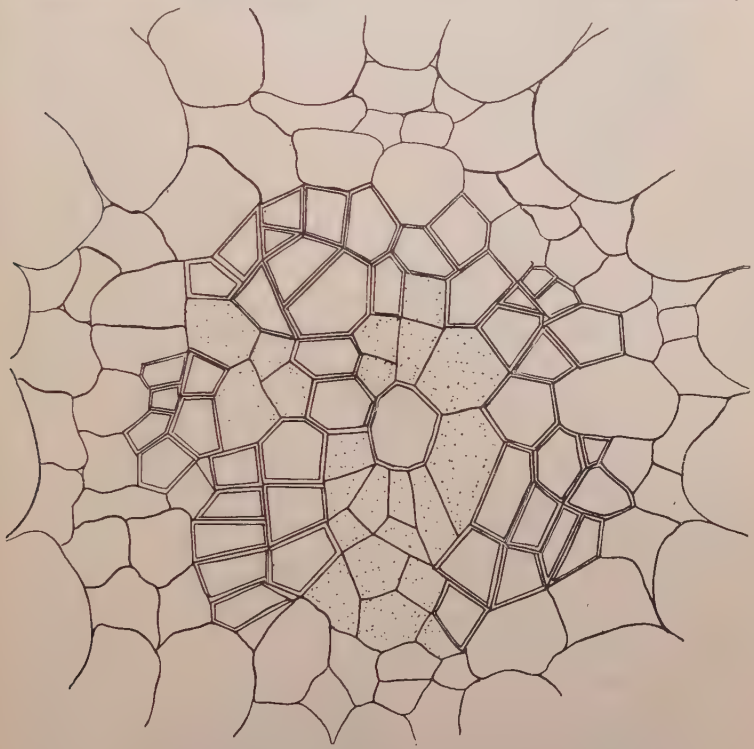

FIG. 35.—*Paris polyphylla*. Transverse section of the hypocotylar stele in a seedling four months old (×450).

the lamina, roughly the same length, is lanceolate and has a strong mid-rib and two parallel traces with ramifications. The subsequent importance of the hypocotyl as a storage organ is indicated by its length in the youngest seedling. Root hairs develop rapidly on the primary root, which is initially short but gradually becomes long, straight, and powerful, tapering towards the tip. It is contractile at an early stage. Neither lateral nor cauline roots appear until the first leaf is above ground and the hypocotyl has become tuberous.

FIG. 36.—*Trillium ovatum*. i–v. Series of developmental stages (seedlings one to four months old) (× 4). vi. Lamina of cotyledon, shrivelled at the suctorial tip (× 2). vii. Longitudinal section of seedling figured in i. viii. Longitudinal section of seedling figured in v. ix–xi. Seedlings of the same age, showing varying degrees of tuberisation (× 2). xii. Longitudinal section of seedling figured in xi. xiii. Longitudinal section of seedling figured in x. xiv. Transverse section of stele towards the mid part of the primary root (× 240). xv. Transverse section of stele at upper limit of the same primary root (× 240).

Anatomy of Seedling.—The root stele may be diarch, triarch, or tetrarch.

Seedling with Tetrarch Root (about three months old) (fig. 37). —The petiole of cotyledon is triangular in cross-section ; the mid-rib is a double bundle, while the two lateral traces are weak. In young seedlings this arrangement holds throughout the entire length of the cotyledon, the tip of which (about 1 mm. long) is embedded in endosperm. In older seedlings the suctorial portion, as it withdraws from the seed, expands and becomes green. In the lamina so formed the three main vascular strands ramify so that a network extends to the tip. The petiole increases in girth towards the sheathing base, which is a storage as well as a sheathing organ. The three strands lie in a ground mass of large, starch-containing parenchyma, with few intercellular spaces. The first leaf makes its way through the cotyledonary wall by rupturing it at its weakest point where there is a thickness of only two or three cells. The three strands supplying the first leaf, and a fourth strand lying between them from the second leaf and plumule, pass from a peripheral to a median position, descending through 0·2 mm. in doing so. Fusion then occurs between the plumular traces, the mid-rib, and the lateral strands of the cotyledon, contrasting with the behaviour of the lateral traces in *Paris.*

The hypocotyl extends through 1·2 mm. and is the most swollen part of the seedling (diameter approximately 1·5 mm.). The epidermal cells are small and regular, cutinised most heavily on the outer tangential wall. The hypodermis does not store starch. The stele is enclosed in a sheath which, lower, becomes defined into a typical endodermis. In the hypocotyl the stele is approximately one-fifth of the total diameter, and consists of six xylem masses, weak phloem, and parenchyma. At the level where the epidermis becomes piliferous the xylem reduces to four patches and the endodermis encloses a compact stele, but the radial arrangement is incomplete. The piliferous region accounts for 0·3 mm. of the total storage region (2 mm. long). In this last fraction of a millimetre the stele becomes typically tetrarch, and the hypodermal layer and three or four rows of cortical cells round the stele are free from starch.

Seedlings with diarch and triarch roots show no essential

difference in the anatomy. The plumular contribution to the diarch root stele is less than in a tetrarch root. The scattered arrangement in the hypocotyl is repeated.

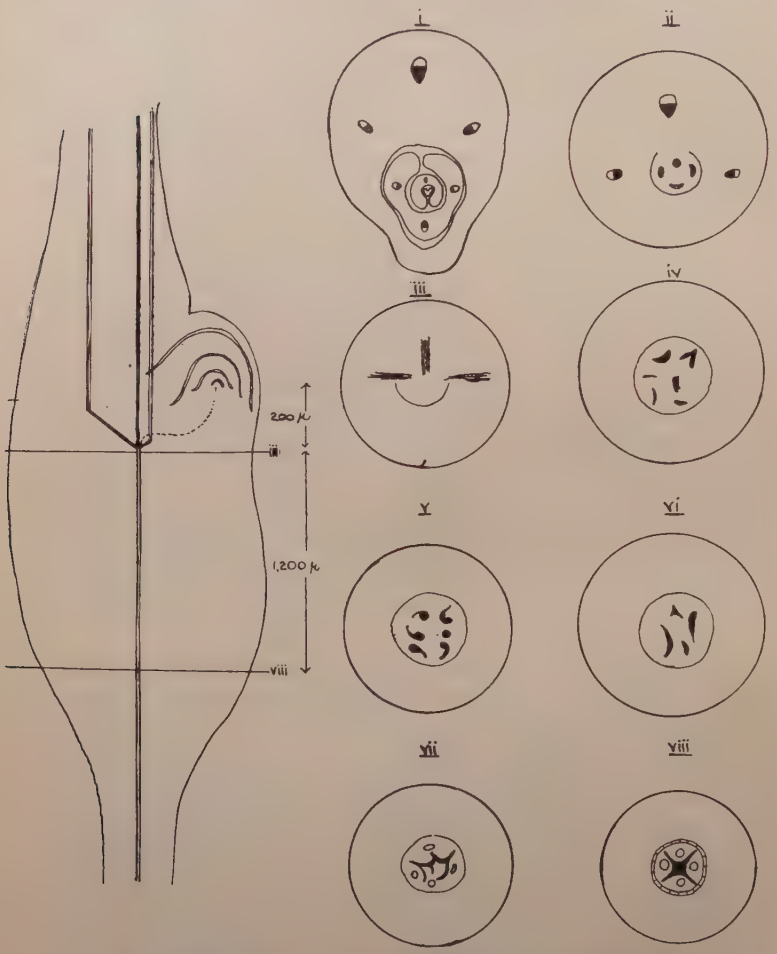

Fig. 37.—*Trillium ovatum.* Vascular skeleton reconstructed from longitudinal sections and tranverse sections i–viii. Hypocotylar anatomy is represented by sections iii–vii.

Development of the rhizome proceeds as in *Paris*. In the very young seedling the hypocotyl is disproportionately long and wide. The swelling of the hypocotyl (fig. 36) appears to be absent in certain seedlings. In such, the first

foliage leaf is produced earlier than in seedlings with a well-stocked hypocotyl.

Sargant (120) quoted *Trillium* as an example of the seedling anatomy of the Medeoleae, but describes only the double bundle of the cotyledon with its pair of laterals. Chrysler (32) finds *Trillium grandiflorum* exhibiting the development of the central cylinder from the protostele to the stage when the strands turn into the medulla and connect with leaf traces. Such features are, in the opinion of the present writer, shown more convincingly by *Paris* than by *Trillium ovatum*.

According to Gatin (58) the trimerous varieties of *Paris quadrifolia* approach *Trillium* in the anatomy of the adult ; the three-leaved variety may be produced for several years before the four-leaved variety of *P. quadrifolia*, and thus the ancestral type appears first. Franchet (50) considers that *Trillium* leads to the three-leaved *P. quadrifolia*, which may indirectly give *P. polyphylla* or other forms. The similarity in the seedlings of the two genera is of interest in connection with this supposed origin of *Paris*.

In addition to seedlings of the rhizomatous species mentioned Sargant (120) also studied those of *Asphodeline*, *Eremurus*, *Bulbine*, *Anthericum*, *Veratrum*, and *Tricyrtis* (see Table IV, p. 200). Chrysler (32) also included seedlings of *Medeola*, *Polygonatum*, *Clintonia*, and *Uvularia* in his research on stelar anatomy. Evans (44) described the germination and anatomy of *Ruscus*, *Danae*, and *Semele*.

Haemodoraceae.

Tribe I. Euhaemodoreae—*Wachendorfia thyrsiflora* L.

The kidney-shaped seed (5–6 mm. × 3 mm.) contains starchy endosperm. The dark brown testa is densely covered by coarse, reddish-brown hairs. Germination is Type C. The seedling has a robust habit (fig. 32, viii). After germination the cotyledon consists of a long, cylindrical or club-shaped sucker (diameter 1 mm.) and a ligule 8–9 mm. in length. The sheathing base of the cotyledon may be suppressed or only 1 mm. or so long ; in the latter instance a short cotyledon stalk of equal length and a distinct hypocotyl are produced. The short, blunt primary root which functions in the first days

of germination is replaced by a system of numerous long, fibrous roots which contain the red dye found in the roots of the adult plant. The first leaf is linear (5 cm. in length).

Anatomy.—The first leaf has three main, and, later, eight subsidiary strands. A single massive collateral strand proceeds from the suctorial tip through the stalk almost to the apex of the ligule. It then descends close to its upward course, and at the base of the first internode fuses with the traces from the first and succeeding leaves. The transition is slow. The xylem becomes consolidated into a closed cylinder, which lower disintegrates into three main masses. The primary root, which is diarch, has an exceedingly strong stele. The early adventitious roots are pentarch.

Wachendorfia paniculata.

Longitudinal sections of seedlings at three stages of development show similar features, with the distinction that the cotyledon has two strands, only one of which is carried into the ligule.

Tribe II. Conostyleae—*Anigozanthos Manglesii.*

The embryo is a minute, almost spherical body lying at the narrow end of a pear-shaped endospermic seed 1·5 to 2 mm. in length. Differentiation in the embryo is poor. Germination is epigeal and the plumular development slow. The cotyledon in the young stages is cylindrical, but later the blade becomes flattened.

Anatomy.—A massive cotyledon strand (fig. 32, ix, x) showing cambial activity proceeds through the entire length of the cotyledon, the ground tissue of which shows little differentiation. The first leaf has five main traces. Immediately below the first internode the cotyledon strand moves towards the centre of the axis and takes up a median position in the stele. The transition at once begins, but is comparatively slow. Numerous adventitious roots are supplied by the stele at the base of the hypocotyl. The primary root has a strong tetrarch stele which lower becomes diarch.

The massive cotyledon strand and stele of the primary root recall *Wachendorfia.*

Tribe III. Ophiopogonoideae.—*Ophiopogon intermedium.*

The seed is spherical (diameter 6 mm.), covered by a pale yellow transparent testa. Germination is Type C. Development of root and shoot is rapid. In a seedling two or three weeks old the long, tapering primary root is 5–6 cm. long, and a short, weak cauline root has been produced; three leaves have then emerged through the ligule of the cotyledon (5 mm. in length).

Anatomy.—Four strands proceed through the cylindrical cotyledon tip (0·3 mm. in diameter), which is embedded in hard endosperm. They all descend through the short sheath, the ligule being non-vascular. Each of the young leaves has a mid-rib and a pair of lateral strands. The cotyledon strands enter the axis at a level when the first and second leaf traces are still distinct. The primary root is hexarch. *Ophiopogon japonicum* has a smaller seed (diameter 3–4 mm.). The cotyledon and first leaf anatomy is similar, but the primary root is pentarch or tetrarch.

Tribe IV. Conanthereae—*Tecophilaea violaeflora.*

The small ovoid seed (1·5 to 2 mm. long) has a brown testa. Germination is Type C. The seedling is slender, the primary root being long and tapering (assisted later by a cauline root) and the leaves linear. The ligule has a maximum length of 5 mm.

Anatomy.—Two simple, sheathed cotyledon strands enter the ligule, bend at the apex, and descend on the opposite side. At the base of the lower sheath, which is 1–2 mm. in length, they fuse with the traces from the first leaf. The latter has a mid-rib and two pairs of lateral strands. The primary root is pentarch.

Amaryllidaceae.

Seedlings of *Alstromeria* sp. were examined. The seed is spherical (3 mm. in diameter) and has a dark brown, warty testa. Germination is Type C. The cotyledon ligule is very short. The plumule rapidly develops, and the second and succeeding internodes are long. The first and second leaves are reduced in size. The third leaf, which has seven

strands, exhibits the shape of the adult leaf. The anatomy of the transition has already been described by Sargant (120). There are two strands in the cotyledon, and the long primary root is diarch.

Iridaceae.

Diplarrhena Moraea.

The seed is small and flattened (1–1·5 mm. in length). Germination is epigeal. The seedling and its anatomy present no peculiar features. The first leaf has a mid-rib and four subsidiary strands, there is a single cotyledonary strand, and the primary root, which at the upper limit is tetrarch, becomes triarch, and finally diarch towards the tip.

Libertia.

Libertia grandiflora.—The pear-shaped seed has a brown testa. Germination is Type B (fig. 26). A slender stalk connects tip and sheath. The latter slits with the development of the first leaves. The cotyledon has a single vascular strand with which three traces from the plumule fuse. The primary root is diarch.

Libertia ixioides differs from *L. grandiflora* in having a much longer stalk connecting the sheath to the cotyledon tip.

Marica humilis Lodd.

The seed is 4 mm. long, flattened on two sides, curved on the third ; the testa is brown.

Germination and seedling as for *Libertia* (fig. 26). The copious production of root hairs, and later of lateral roots, and the lengthy first node are noteworthy.

Anatomy.—There is one strand in the tip of the cotyledon but three in the sheathing base. An endodermal sheath extends half round the central cylinder before the cotyledonary traces enter it. The root stele is polyarch and in older seedlings becomes markedly sclerosed.

Iris.

The following species provided material for examination :—

Iris Chamaeiris
,, *ensata*
,, *germanica*
,, *Nertchinskii*
Iris Pseudacorus
,, *stolonifera*
,, *Swertii.*

The appearance of the cotyledon is variable (fig. 38). Rendle remarks that three of Klebs' types are represented ; *Iris Pseudacorus* conforms to the type with sword-shaped

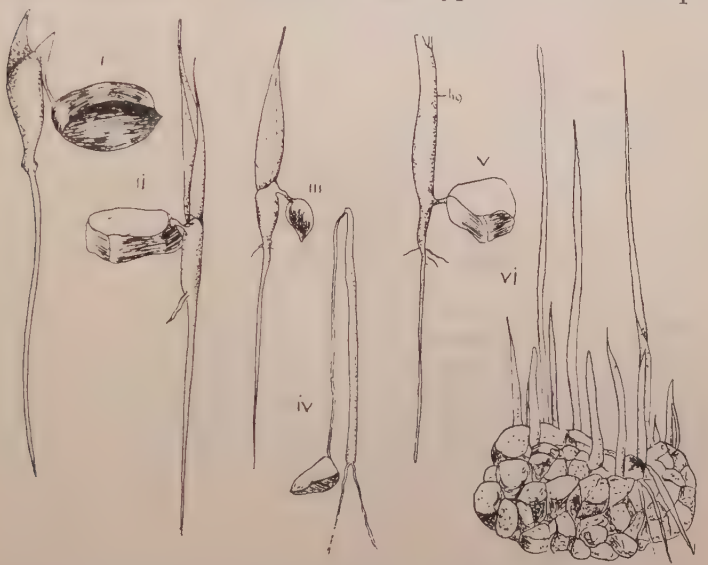

Fig. 38.—Seedlings of species of *Iris*. i. *I. Pseudacorus* ($\times\frac{3}{2}$). ii. *I. Nertchinskii* ($\times 2$). iii. *I. stolonifera* ($\times 2$). iv. *I. germanica* (actual size). v. *I. ensata* var. *pabularia* ($\times 3$). vi. Mass of seeds from ripe capsule of *I. germanica*, showing viviparous germination (actual size).

cotyledon sheath ; *I. sibirica* (=*I. setosa*) " affords instances of the second type, which is the more general one in the order, showing a more complete differentiation of the cotyledon into a sheathing base and an absorbent tip, the two parts being connected by a slender portion. The third or epigeal type, where the cotyledon . . . forms the slender, tapering first green leaf . . . has been described in a species of *Iris* " (110). No essential difference between Rendle's first and second types exists. The third type was not encountered in the present research.

The length of the sheath averages from 2 to 5 mm. The connecting stalk may be very short or exceedingly long, but the germination of *I. germanica* shows that no significance can be attached to this, since the lengths of the stalk and hypocotyl are inter-dependent. Germination in *I. germanica* (fig. 38, vi) may be viviparous, the elongation of the hypocotyl being a means of propelling the upper part of the seedling between neighbouring seeds and through the decaying capsule wall. In certain seedlings of this species the plumule does not emerge after the primary root, but develops inside the seed coat, which it pierces at the end remote from the micropyle. One species (*I. ensata* var. *pabularia*) produced a ligulate cotyledon.

Anatomy.—The cotyledon has either a double bundle, a single bundle, or a single bundle becoming double towards the base. The primary root may be diarch, triarch, or tetrarch. The number of strands in the first leaf is variable ; seven or nine strands are commonly found.

Sisyrinchium.

Seedlings of *S. californicum*, *S. pachyrhizum*, and *S. striatum* were investigated. Germination is epigeal. Each has a long, filiform cotyledon with a double bundle and a lengthy primary root which is diarch. Three strands are found in the first leaf, which is ensiform.

Holm (79) found in the genus a striking similarity in the anatomy of the adult, a research suggested by the tendency at the time (1908) to raise Bentham and Hooker's three sections, Bermudiana, Echthronema, and Eriphilema, to generic rank, a procedure which Holm, from his anatomical studies, considered unjustifiable.

Seedlings of species of the first section were not investigated. *S. striatum* and *S. pachyrhizum* in the second section are indistinguishable from *S. californicum* in the third. The three species agree in external morphology with *S. angustifolium*, described by Holm, who unfortunately adds no anatomical data.

Aristea Ecklonii.

The cotyledon is ligulate and resembles that of *Tigridia Pavonia* in having a sharp angle between the stalk and sheath-

ing base. The seedling is anatomically simple, there being a single cotyledon strand extending for a short distance in the ligule, and triarchy (lower, diarchy) in the primary root. The first leaf has a mid-rib and two lateral strands.

The adult plant is of the erect herbaceous type with a short, thick, oblique root stock, and belongs to a genus containing two of the four shrubby Iridaceae, namely, *A. corymbosa* and *A. fruticosa* (132). No indication of such a relationship is afforded by the seedling.

Commelinaceae.

Members of this family are annual or perennial. Seedlings of plants of the former group should not legitimately be described with plants having rhizomes, but the germination and seedling structure of the Commelinaceae is essentially uniform for annuals and perennials.

The early work of Solms-Laubach (135) on the embryo of Commelinaceae, and his discovery that the plumular bud was apparently terminal, gave rise to speculation on the homology of the cotyledon. Schlickum (127) described the anatomy of *Commelina coelestis*, Willd., and *Tinantia erecta*. Holm (78) gave a brief account of the seedling of *C. nudiflora* without fully describing the anatomy. Hollinshead (74) published detailed notes on the germination of *C. communis* L., but omitted the anatomy of the hypocotyl.

Tinantia fugax.

The seed varies in shape according to its position in the capsule and the number of seeds present. It is generally roundish or cubical, having a diameter approximately 2·5 mm., covered by a black, leathery, warty testa. A small circular lid is pushed out by the radicle on germination. The abundant endosperm is starchy. Germination is hypogeal (fig. 39). The cotyledon consists of a long sheathing base connected to the suctorial tip by a slender, thread-like stalk. The length of the latter depends on the depth of the seed in the soil, since it keeps pace in elongation with the growth of the sheath and hypocotyl, the seed remaining at its original level. Growth is rapid. The first leaf emerges at the apex of the sheath,

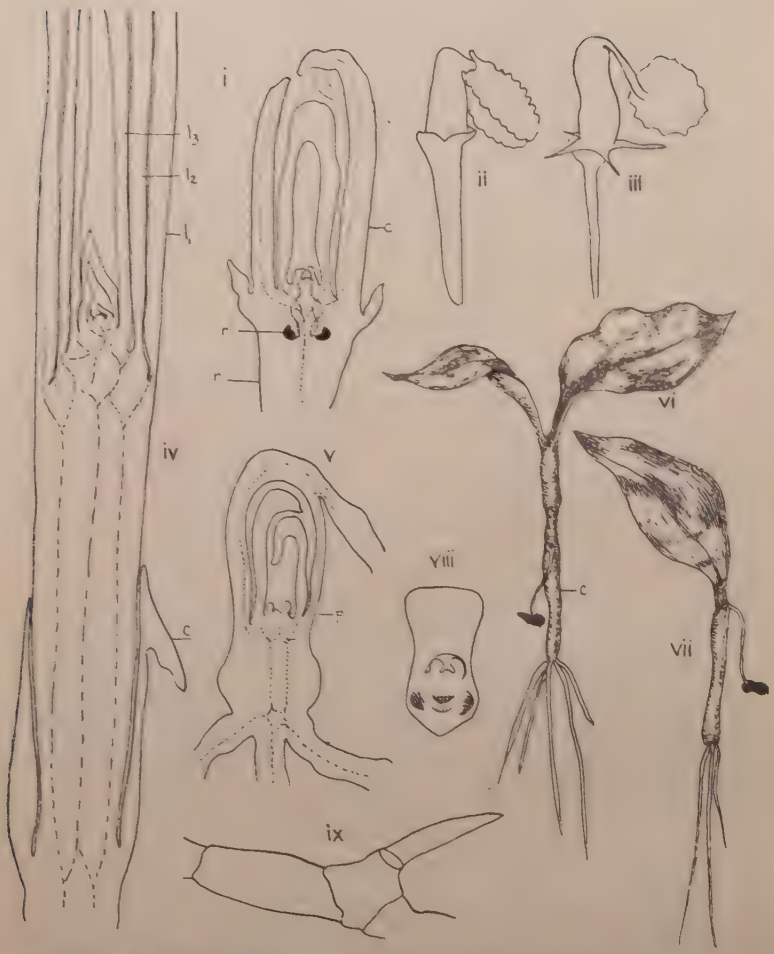

FIG. 39.—*Tinantia fugax*. i. Longitudinal section of seedling two days old (×20). ii–iii. Seedlings less than a week old (×5); the ring of adventitious roots have appeared in the older seedling. iv. Longitudinal section of seedling figured in vi, showing the symmetrical vascular system (×10). v. Longitudinal section of seedling a week old, showing the marked development of the hypocotyl and adventitious roots (×20). vi–vii. Seedlings two and three weeks old (actual size). viii. Ripe embryo dissected out from the seed, with plumular bud and three adventitious roots in focus (×30). ix. Multicellular hair from epidermis of first leaf (×150).

c = cotyledon; l_1, l_2, l_3 = first, second, and third leaves; p = level of plumular bud; r = primary root; r' = adventitious root.

which is ligulate, and appears above ground during the first week, being followed before six weeks have elapsed by a succession of four or five leaves. The well-developed primary root is soon surrounded by four adventitious roots, arising equidistantly from the base of the hypocotyl. Four others are later produced, alternating with and immediately above the original four. The hypocotyl is at first difficult to distinguish. After a week it is discernible as a cylindrical, smooth, semi-transparent structure, widening at the upper limit, constricted very abruptly at the lower limit. For some time it continues to increase in length.

The first leaf is obovate to lanceolate ; when fully expanded the blade is 2 cm. long and 1·5 cm. at its maximum width and has a mid-rib and two to four pairs of lateral strands, the number depending on its age. Multicellular hairs arise obliquely on the margins and upper surface of the blade (fig. 39, ix).

Anatomy.—Two strands run parallel through the stalk of the cotyledon. One immediately descends to the base of the sheath ; the other ascends to the apex of the short ligule, and descends on the opposite side of the sheath. At the base of the cotyledon both strands tend to converge. Still independent, they continue their course in a central position to the base of the hypocotyl, appearing in transverse section as two wedges (fig. 40).

At the base of the first node the mid-rib bifurcates, providing two strands in the hypocotyl. The lateral strands of the first leaf fuse in pairs, which unite at the upper limit of the hypocotyl only to be halved again. The second pair of plumular traces originate from the subsidiary strands of the first leaf. The four plumular traces are disposed like the corners of a square about the cotyledon traces. The tetrarch root stele at the base of the hypocotyl is formed entirely from the cotyledon strands. Each plumular strand is in direct continuity with an adventitious root, the internal structure thus accounting for the regularity with which these roots arise. Since the plumular strands have no connection with the primary root, the necessity for adventitious roots is apparent. It is also clear that the primary root need not increase in length or girth, since the plumule makes no demands upon it. This arrangement, whereby the first leaf is made independent of

the radicle, is initiated in the embryo (fig. 39, viii), which differentiates the meristem of the four adventitious roots. The cotyledon sheath in a six-weeks-old seedling (fig. 39, iv, vi) still

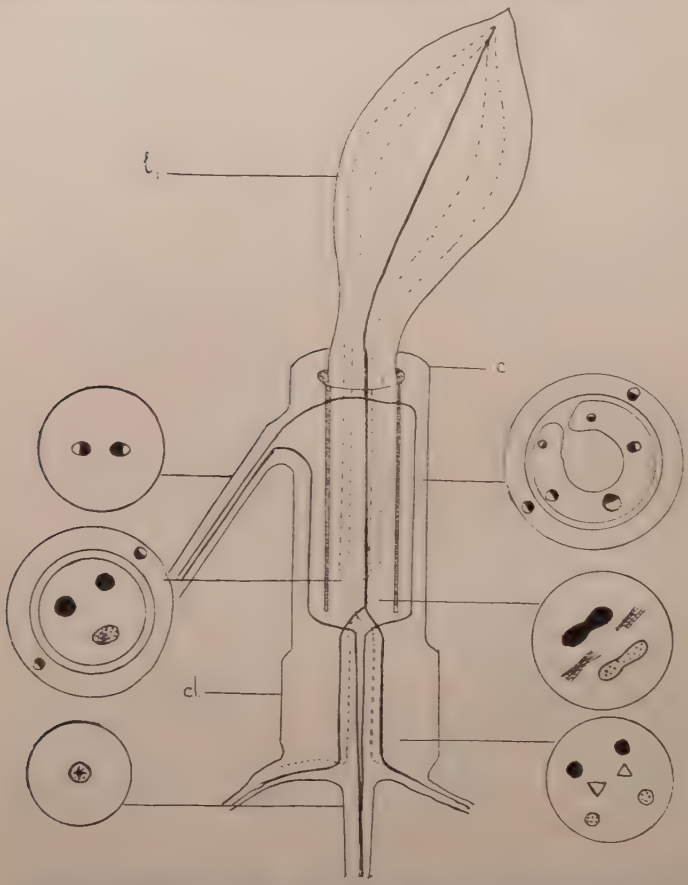

FIG. 40.—*Tinantia fugax*. Vascular skeleton reconstructed from longitudinal and transverse sections.
c = cotyledon ; cl = " collet " ; l_1 = first leaf.

surrounds the lowest internode. In the stem there are ten central and sixteen peripheral closed bundles. A swollen region indicates their fusion with the cotyledon bundles. There are four strong vascular strands in the hypocotyl, at the upper limit of which four cauline roots emerge. Four root initials alternate with them.

Seedlings of *Commelina coelestis*, *C. dianthifolia*, *C. graminifolia*, *Cyanotis cristata*, *Rheo discolor*, *Palisota Pynaertii*, and *Tradescantia geniculata* var. *Kunthiana* were also examined. There was a general uniformity in the anatomy except in the primary root of *Cyanotis* and *Tradescantia*, both of which had triarch steles. Multicellular hairs are found on the cotyledon and leaves of *Tradescantia* and *Palisota*, while the cells of the abaxial epidermis of the cotyledon and leaves of *Cyanotis* and the three species of *Commelina* were markedly papillose.

Cannaceae.

Canna indica L.

Hegelmaier (66) and Humphrey (82) have described the seed and embryo. The seed is spherical or ovoid, 8 mm. long. The hard, thick testa projects into the perisperm, forming a micropylar collar which surrounds part of the embryo. Stomata occur in the testa (82). A thin aleurone layer, the true endosperm, is enclosed by a mass of starchy perisperm. The embryo at maturity is highly differentiated. Three leaves and the rudiments of numerous adventitious roots may be defined. The sucker of the cotyledon is a thick, cylindrical organ widening towards the rounded tip. A slight constriction separates it from the remainder of the embryo, which is asymmetrical and lies partly in the micropylar canal. The plumule and radicle, like those of *Billbergia*, are not in alignment. Their axes lie at an obtuse angle. The vascular skeleton is therefore strongly asymmetric. Humphrey stated that Hegelmaier's observations on the rupture of the testa at germination are faulty. Germination is Type C. The radicle pushes out a circular lid, which breaks off round a line of weakness in the testa.

Anatomy of Seedling a Day Old.—At this stage the ligule of the cotyledon has not developed. In the tip of the cotyledon, which is 1·5 mm. in diameter, twenty traces are peripherally arranged. At a constriction formed by the micropylar collar they unite, forming four, five, or six strands, which beyond this region increase to seven or eight and enter the sheath. There are ten strands in the first leaf; two leaf strands apparently fuse with each cotyledonary trace. At a

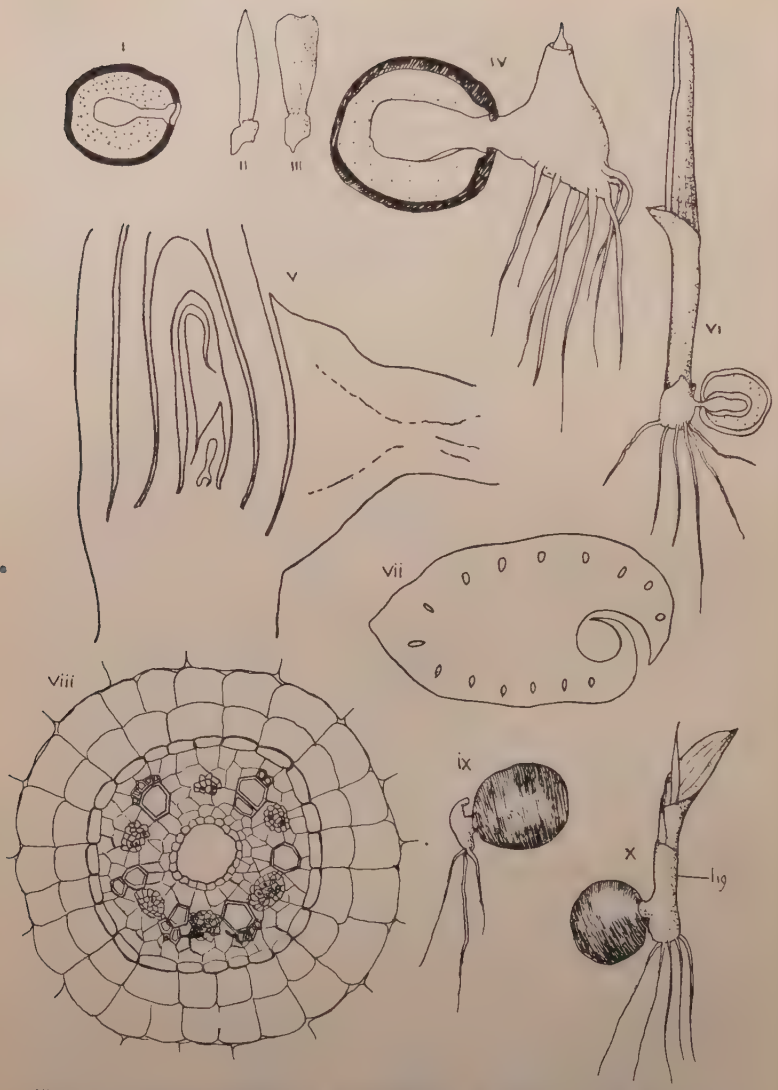

FIG. 41.—*Canna flaccida*. i. Longitudinal section of ripe seed (×3). ii–iii. The asymmetric embryo in lateral and surface view (×5). iv. Young seedling, showing the apex of the first leaf appearing through the ligule and the copious supply of adventitious roots (×5); the seed has been cut to show the development of the sucker. v. Longitudinal section, showing young leaves, part of cotyledon ligule, and sucker of seedling figured in iv (×15). vi. Seedling of *Canna* sp. with two foliage leaves above the surface (×$\frac{2}{3}$). vii–viii. *Canna flaccida*. vii. Transverse section of first leaf (×12). viii. Stele and part of the cortex of adventitious root (×150). ix–x. Seedlings of *Canna indica* (×2).

level when half of the cotyledonary strands are still independent, adventitious roots are initiated. A crescent of such roots arises at the level where cotyledon and plumular strands completely unite. It was impossible to follow the transition, which must be extremely rapid, nor could the structure of the primary root be determined. Gatin (53) remarked on the endogenous origin of the latter. Even after germination it is

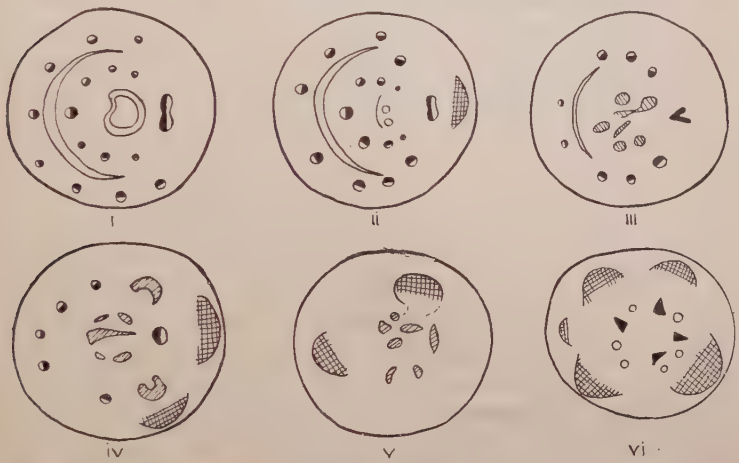

FIG. 42.—*Canna indica*. Transverse sections of seedling a day old. i. Base of first internode. v. Final passage of cotyledon strands to centre of axis; origin of numerous adventitious roots. vi. Base of axis, showing five adventitious roots.

undeveloped, or, if it develops, cannot be distinguished from the adventitious roots, of which there are at least nine or ten.

Gatin (53) figures the embryo and germination of *C. indica*, and Tschirsch (149) the longitudinal section of the ripe embryo. The former notes the large number of cotyledonary strands in the embryo; fourteen are placed round the plumular bud, but there are eleven arranged in a semi-circle in the hypocotyl. Schlickum (127) finds that of twelve strands leaving the cotyledon tip half pass into the ligule; ten or twelve strands occur in the first leaf, and sixteen in the second leaf.

Canna flaccida.

The ligular development of the cotyledon is less pronounced in *C. flaccida* (fig. 41). There are twenty strands in the

suctorial part of the cotyledon but only five in the ligule. Fifteen strands with interlying aerenchymatous spaces are found in the first leaf, which has a simple linear shape: the second leaf has a broad blade, tapering sharply towards the apex and seven main and eight subsidiary strands. A blunt projection indicates the end of the root axis although its anatomy could not be determined. The adventitious roots have a hexarch stele, with very large metaxylem elements and a central cavity. The endodermal cells are small and arranged with a regularity which is repeated by the inner half of the cortex; the cells of the latter are rectangular in shape, with rounded corners (fig. 41).

Canna sp. 301.

The ligule of the cotyledon is long (3–4 mm.) and wide. Four layers of endosperm cells, a tannin layer, and copious perisperm surround the suctorial tip, which has fourteen strands arranged in pairs; they reduce to nine traces at the micropyle. Of the nine strands four or five strands are found in the ligule before they descend to the base. The first leaf is smaller than the second; they have eleven and thirteen strands respectively.

ZINGIBERACEAE.

The rhizomatous habit is common to all members of this family of perennial herbs, although the form of the rhizome is variable. Engler divides the family into—

A. Sub-family ZINGIBEROIDEAE:

Tribe I. HEDYCHIEAE
Tribe II. GLOBBEAE
Tribe III. ZINGIBEREAE.

B. Sub-family COSTOIDEAE.

The distinction between the sub-families is shown by their seedlings.

A. ZINGIBEROIDEAE.

The seed is almost spherical, with an average diameter of 4 mm. Lubbock (97) takes *Elettaria speciosa* as typical of

Amomum and *Alpinia*, and mentions the lid-like stopper lying opposite the hilum which is pushed out by the emerging primary root. No description of the seedling is given. Humphrey (82) chooses *Costus* as the basis for discussion of the seed of the family, remarking that "in the presence of the micropylar collar and germinal lid, and in the development of embryo and endosperm, all the forms examined agree closely." Humphrey figures the ripe seed of *Amomum* as having a germinal lid. Although the germination has not been followed from the initial stages by the writer, the stalk of the cotyledon obviously emerges from the seed at a clean-cut circular aperture. But the presence of a germinal lid in *Alpinia calcarata* and other Zingiberoideae investigated by the writer is less clear. The testa is ruptured along lines of weakness, running out from the hilum, so that a collar of five or six ragged triangular teeth edge the opening through which the primary root appeared. The seed coat of the Zingiberoideae examined resembles that of *Costus*, which Humphrey describes. The outer integument gives rise to three layers, namely, an outer compressed sclerotic layer, a very narrow nutrient layer, and an inner band of large mechanically effective cells, elongated radially, thickened on all but the outer tangential wall. The bulk of the food reserve is starchy perisperm, of which the cells are radially elongated. A layer of cells containing tannin separates them from the true endosperm, which is aleurone. Whether the intermediate tannin layer occurs before absorption of food reserve takes place was not investigated. It is not mentioned by Humphrey as occurring in *Costus* and *Amomum*.

The vascular system of the embryo is asymmetric. Germination is of the pronounced ligulate type described for *Canna*. It is often difficult to determine the structure of the primary root, which is endogenous in the embryo and may not exist as a separate root, or function only in the initial stages of growth. The massive root sheath which is conspicuous in the young seedling recalls the coleorhiza of the Grass seedling. Adventitious roots invariably appear a few days after germination. The sheathing base of the cotyledon is reduced almost to extinction, and in all but *Amomum* the stalk connecting the suctorial tip to sheath and ligule is almost completely suppressed. The cotyledon may, therefore, be

regarded as mainly consisting of a cylindrical or spindle-shaped suctorial tip and a well-developed ligule. The plumule is the dominant organ of the seedling : the third leaf rudiments can be distinguished in a seedling two days old, at which stage the primary root is represented by the blunt basal end of the embryonic plant. Five days later the first leaf pierces the apex of the cotyledon ligule. After a week or so, buds are found in the axils of leaves.

Tribe I. Hedychieae—*Cautleya lutea.*

Anatomy.—The seedlings had a hypocotyl unusually long for the sub-family and a distinct primary root. The first leaf has a mid-rib and two pairs of lateral strands. The traces of the early leaves run through the first internode as a central cylinder, but the first leaf traces remain independent in the periphery. There are two cotyledon strands. One ascends to the tip of the ligule, bends very sharply, descends on the side remote from the sucker, and appears to fuse with the two right-hand lateral traces of the first leaf before it merges into the central mass at the base of the first internode. The other strand proceeds horizontally from the sucker to the centralised plumular strands in the internode. As it does so, it passes between and unites with the left-hand lateral traces of the first leaf. The cotyledon strands are, therefore, in their ultimate behaviour identical.

Two interpretations are possible. The lateral traces of the first leaf may be regarded as proceeding downwards and placed in a position favourable for communication with sucker and central cylinder ; or it may be held that each cotyledon strand splits in the periphery of the internode, giving two upward branches (the lateral traces of the first leaf), the remainder passing to the central cylinder. In almost every Monocotyledonous seedling examined it is usual for the lateral traces of the first leaf to lose their identity by merging into the central vascular cylinder or by fusing with the mid-rib before or when the latter does so. For this reason the exceptional condition of the lateral traces in *Cautleya lutea* would seem to be due to their direct origin from the cotyledon strands.

The stele of the primary root is triarch.

Hedychium Gardnerianum.

Anatomy of Two-days-old Seedling.—At this stage the axis of the seedling was curved, and ligular development had not

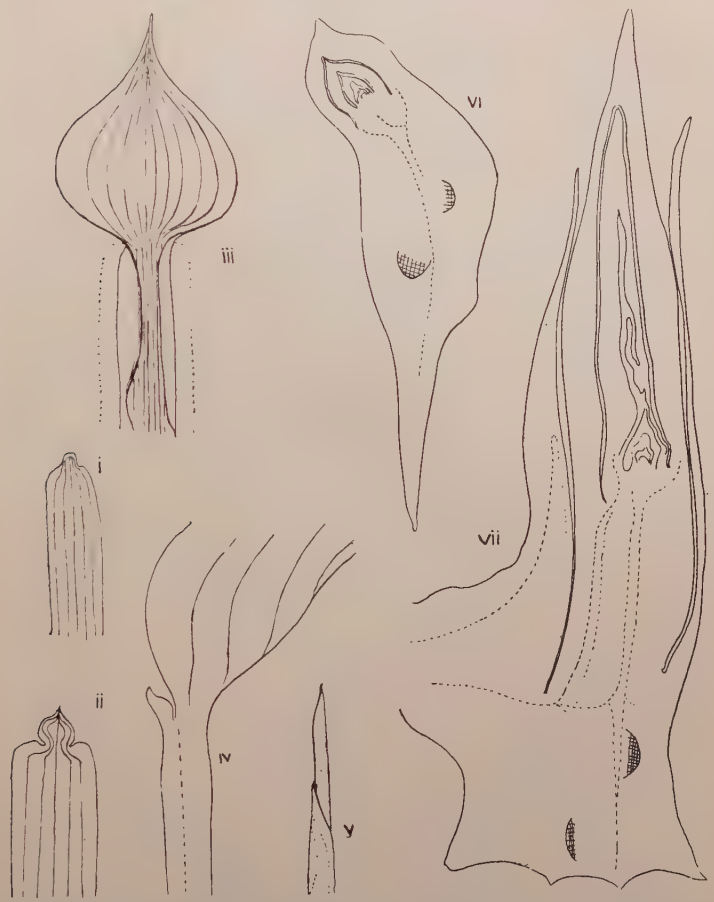

Fig. 43.—*Hedychium Gardnerianum.* i–iii. First three leaves of the seedling (×6); the dotted lines in iii indicate the position of the sheath reflected back. iv. Lateral aspect of third leaf, showing the ligular outgrowth towards the upper limit of the sheath (×6). v. Fourth leaf convolute in the bud. vi. Longitudinal section of seedling two days old; the meristem of two adventitious roots is seen (×20). vii. Longitudinal section of seedling with fully developed cotyledon ligule (×20). (See also figs. 66, 68.)

commenced. The anatomy is exceedingly simple (fig. 43, vi). Two strands leave the cotyledon tip. In the uppermost part of

the sheath, which will ultimately produce the ligule, one strand divides in two, but the halves reunite above the plumular bud. Only three traces are differentiated in the first leaf,

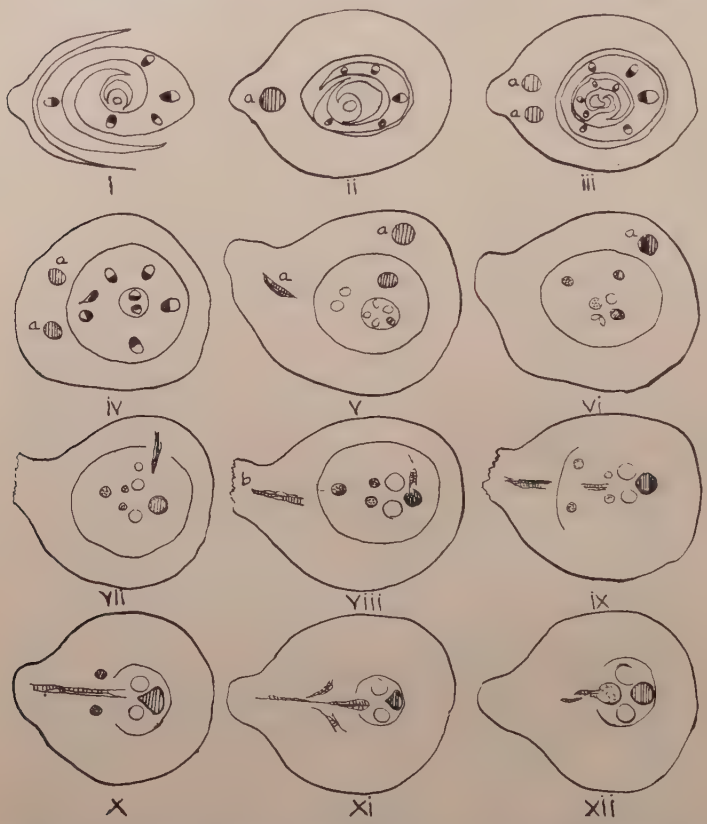

Fig. 44.—*Hedychium Gardnerianum*. Transverse sections of seedling six days old from plumular bud to hypocotyl. i. Plumular bud and tip of ligule. ii. Level at which the ligule strand bends downwards (marked *a*). iii. Upward and downward passage of strand in ligule (*a*, *a*). v. Passage of ligule strand from sucker. vii. Passage of ligule strand, after completion of downward course, into central cylinder. viii. Passage of second cotyledon strand from sucker. ix–xii. The second strand enters the internode. xii. Upper limit of hypocotyl.

and the combined cotyledonary and plumular traces amount to four. A scattered arrangement prevails in the hypocotyl. The primary root is tetrarch. The only unusual feature in the anatomy is the splitting and subsequent fusion of the elements of one cotyledonary trace.

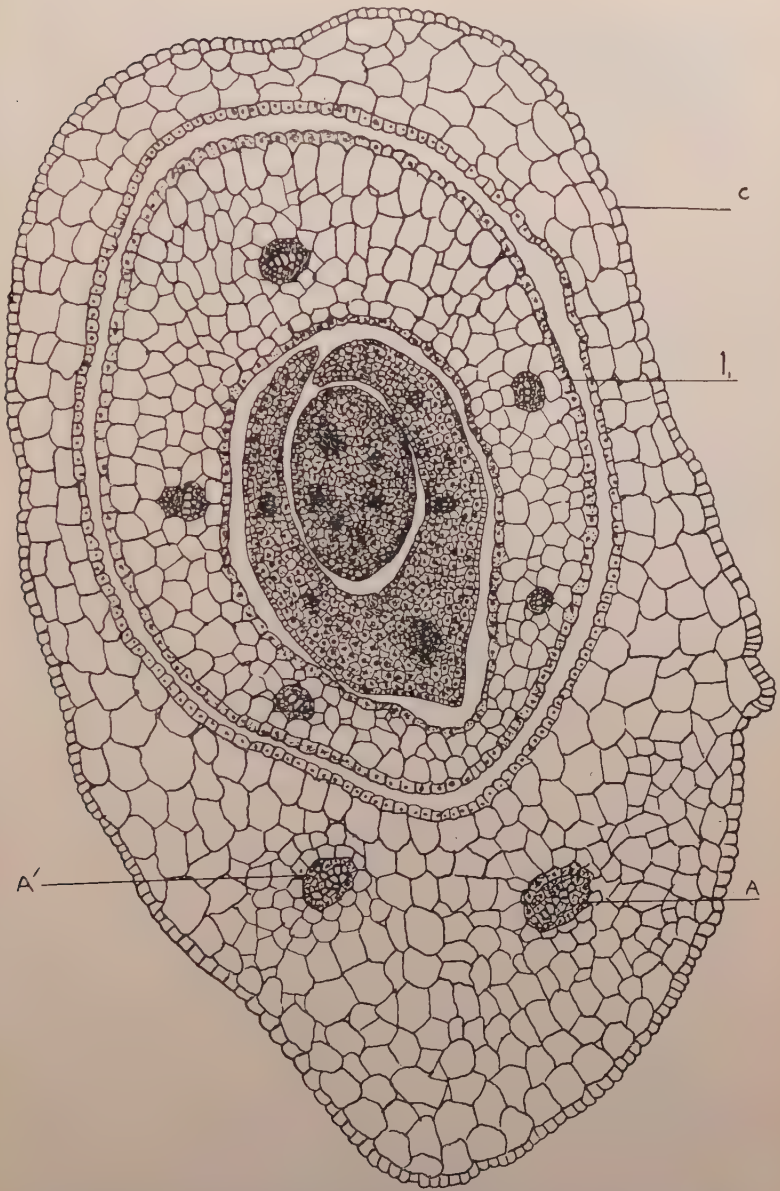

FIG. 45.—*Hedychium Gardnerianum.* Transverse section above the upper limit of the first internode, showing the bases of the first three leaves (l_1, etc.) and the cotyledon ligule (c); A and A′ represent the upward and downward passage of the strand entering the ligule (× 80).

Seedling One Week Old (fig. 44).—Two vascular strands diametrically opposed proceed horizontally from the tip of the cotyledon through the short stalk and diverge (fig. 44). Strand (*a*), the upper, enters the ligule, turns vertically

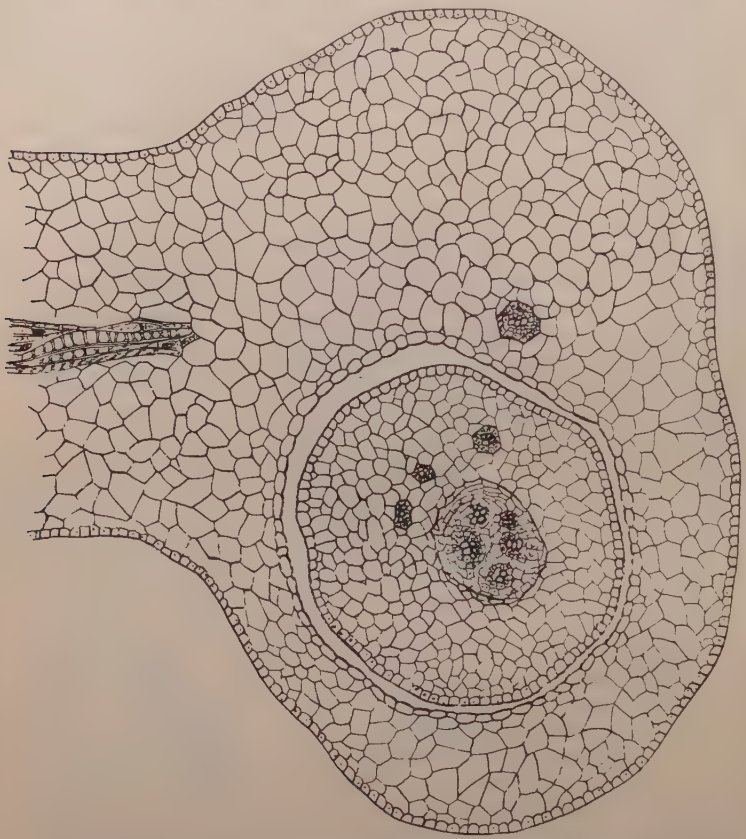

Fig. 46.—*Hedychium Gardnerianum*. Transverse section at the level at which the strand *a* proceeds from the cotyledon sucker to ascend in the ligule ; its downward course is seen in transverse section (× 60).

upwards, bends very sharply when half-way up, and descends almost vertically (fig. 45). At the base of the first internode the downward trace enters the axis, sends a branch upwards, passes inwards, and fuses with a xylem group supplying the mid-rib of the first leaf. Strand (*b*) does not enter the ligule : it continues in a horizontal direction, entering the axis at the base of the first node, which is placed on the level of the stalk

and seed (fig. 47). There it gives off two branches which ascend the first internode, maintaining a peripheral position on the side nearest the seed, finally providing the first leaf with its two outermost pairs of traces. After branching, the remainder of the original strand (*b*) proceeds farther

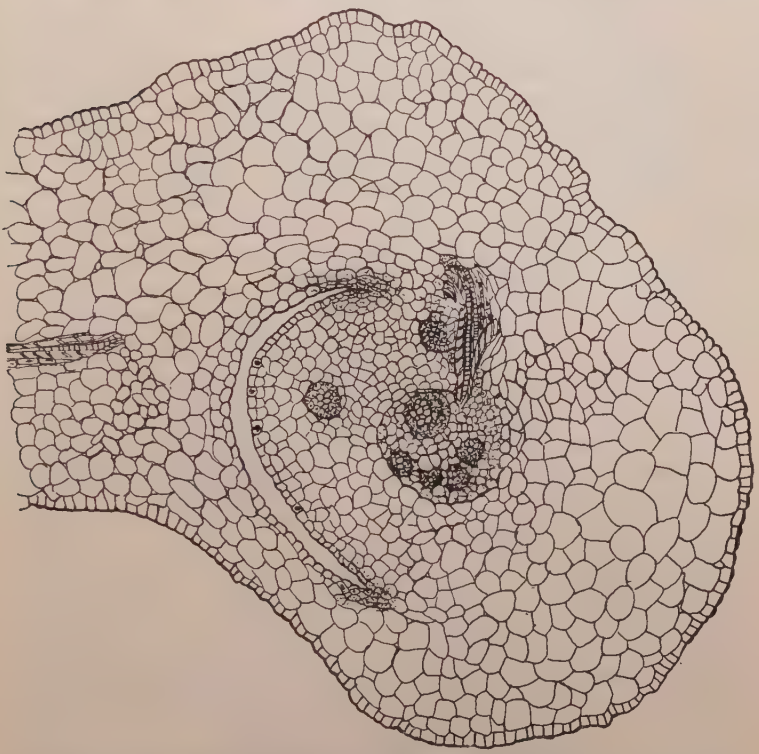

FIG. 47.—*Hedychium Gardnerianum*. Transverse section at a level lower than in fig. 46. Cotyledon strand *b* is seen proceeding from the sucker, while strand *a*, having completed its downward course, is entering the internode, giving off two branches as it does so (× 60).

inwards, sends another pair of branches upwards, and fuses with the strands of the plumular axis without departing perceptibly from its horizontal course ; the greater proportion of its elements then proceed downwards.

The first leaf is provided with a mid-rib, two pairs of strong and an outer pair of weak lateral strands. The ring of five strands which are therefore found at its base are in direct connection, in the first instance, with strand (*a*) on

completion of its course, and almost immediately by that part of strand (*b*) which does not run upwards through the internode. Below the cotyledon stalk (and, since the cotyledon strands have lost their identity, in a region which may

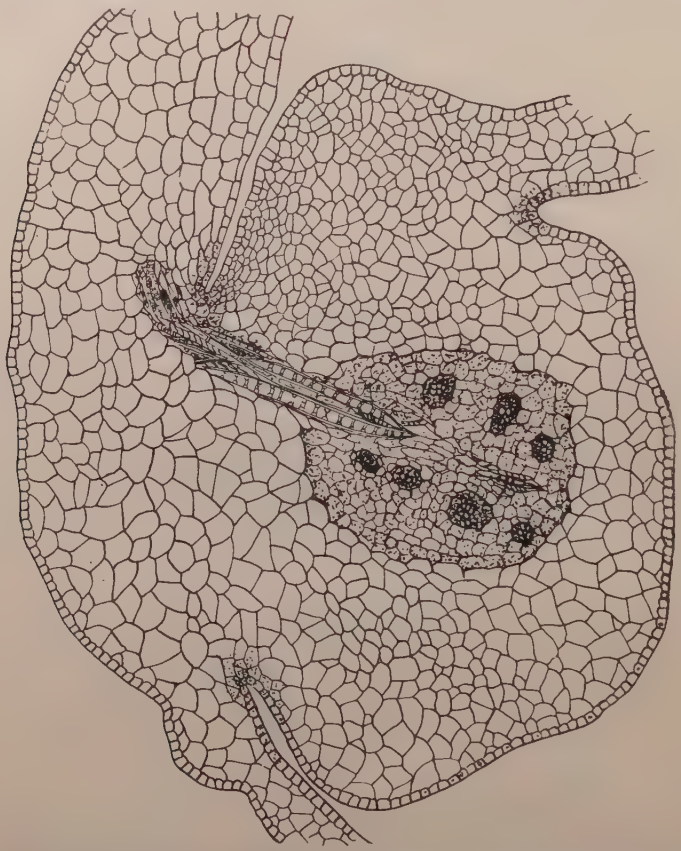

FIG. 48.—*Hedychium Gardnerianum*. Transverse section towards the base of the first internode, showing the passage of strand *b* (which does not enter the ligule) from the cotyledon sucker into the internode (× 60).

be regarded as hypocotyl) the strands are resolved into four groups. That nearest the cotyledon stalk is comprised of the independent portion of strand (*b*) and the outer laterals of the first leaf. The vertically opposite group is derived chiefly from strand (*a*) and the mid-rib of the first leaf. Lower, there results a symmetrical pattern of four quadrants separated by parenchyma. In each quadrant xylem surrounds

the phloem on two sides. Rotation and fusion give a tetrarch root. Longitudinal sections confirm these observations (fig. 43).

Morphology of the First Leaves.—Adopting Rendle's nomenclature (110) for the parts of the adult Zingiberaceous leaf ("sheath, stalk, and blade, with ligular outgrowth of the sheath") the following sequence arises. The first leaf is entirely sheath and completely enfolds the younger leaves. It is linear, with a rounded hood-like apex (fig. 43). Its midrib and two pairs of parallel subsidiary strands are supplemented by another pair as the girth of the seedling increases. The second leaf (fig. 43) is mainly a sheath. Towards the apex a deep constriction occurs, beyond which there is a small, leaf-like tongue. The veins run uninterruptedly to the tip. The two flaps of tissue below the constriction, although not the wings of the ligule, foreshadow the adult form. The third leaf, the blade of which is convolute in the bud, attains the adult form. The sheath has the appearance and length of the first leaf. The hood-like ligule, which completely covers the sharp tip of the fourth leaf, projects at its upper limit, and is formed of two wing-like projections of the margins of the sheath, which, in the normal position, overlap and coil one on another. The blade is obovate lanceolate, and the veins, which are parallel in the sheath, converge at the constriction between sheath and blade (where a stalk occurs in leaves possessing such), then bend out towards the margins of the blade, and again converge at the sharp tip.

Hedychium coccineum var. *carneum.*

The testa is black and not reddish brown as in *H. Gardnerianum*, and the third and succeeding leaves of this species and *H. spicatum* have a short stalk.

Roscoea.

Roscoea purpurea.—Sargant and Arber (124) describe the cotyledon as having an upper (*i.e.* ligular), but in certain instances no lower sheath. They found two cotyledon strands, and root plates and cauline roots above the first node. The cotyledon anatomy is regarded as similar to that of *Elettaria*

Cardamomum Maton., in which, it is stated, both cotyledon strands follow in the ligule an asymmetrical course. In two seedlings which had no lower sheath the authors record that one vascular strand runs into the stele of the axis; its subsequent behaviour was not followed.

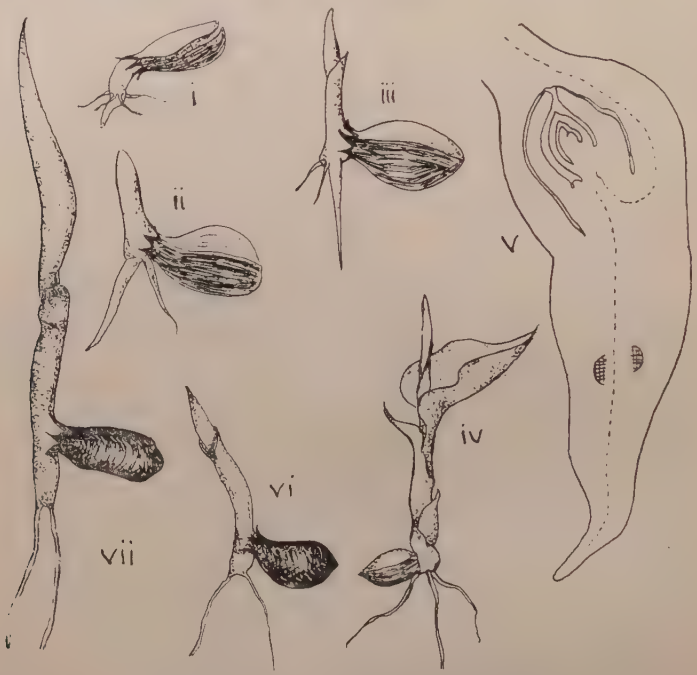

Fig. 49.—i–v. *Alpinia calcarata*. i–iii. Seedlings less than a week old (×5). iv. Seedling two or three weeks old, showing succession of leaves (×2). v. Longitudinal section of seedling a day old; the cotyledon ligule will develop from the tissue which forms a slight elevation on the sheath, dorsal to the seed. vi–vii. Seedlings of *Roscoea cautleoides* (×4).

In the three seedlings of this species examined by the writer only one vascular strand entered the ligule: it ascended to the apex and descended on the opposite side, entering the first node at the base of the ligule. The second strand proceeded directly from the sucker to the base of the plumular axis. Both strands provide the lateral traces of the first leaf in the manner seen in *Cautleya lutea*. The hypocotyl stele, which is sheathed, has a scattered arrangement. The primary root is triarch.

Roscoea cautleoides (fig. 49) shows the same internal structure. The sheathing base of the cotyledon of the seedlings studied was approximately one-third the length of the ligule. The first internode is comparatively long. The primary root stele is diarch.

Roscoea alpina, in which the cotyledon is anatomically similar, has a primary root stele which is triarch at its upper limit, but passes into diarchy, then a mon-arch arrangement at its tip.

Berridge (9) observed mesarch bundles in the cotyledon tip in *Roscoea*, *Alpinia*, and *Brachychilum*, but decided against their being of phylogenetic value.

Brachychilum Horsfieldii.

Sargant and Arber described the cotyledon as "inserted partly on the sheath and partly on the axis," thereby indicating that the cotyledon has a ligule but no sheathing base. In three seedlings examined by these authors neither cotyledon strand entered the ligule ; in a fourth, one bundle curved upwards for a short distance into the ligule "before turning back into the axis." The upper hypocotylar anatomy but not that of the first internode was described.

The writer prepared longitudinal microtome sections of two seedlings at different stages of development but no transverse sections. Unfortunately, attempts this season to germinate seeds have proved unsuccessful, but it is clear from the preparations of the younger seedling (in which the ligule is just beginning to arch up) that the cotyledon anatomy is then essentially the same as that of *Roscoea* and *Cautleya*. Only one strand passes into the ligule, but both are directed horizontally into the centre of the axis immediately below the plumular bud : at this stage elongation of the young internodes has not occurred. At a later stage the plumular bud is carried up by elongation of the second internode ; the first internode remains short. The primary root had not developed in either seedling.

Tribe III. Zingibereae—*Alpinia calcarata.*

Sargant and Arber (124) note that the first leaf is preceded by a "sheath," but the mature form is not apparent in

either the first leaf (the " sheath " referred to) or the second. Because two strands proceed from the cotyledon tip and the plumule provides three endarch bundles it was assumed that the hypocotylar anatomy was the same as for *Brachychilum Horsfieldii*.

Anatomy.—If the ligule of the cotyledon be flattened out and examined, it is seen to be without vascular tissue,

FIG. 50.—*Alpinia calcarata*. Transverse sections of seedling a few days old. viii. Primary root. vi. Two cotyledon strands, *a* and *b*, proceeding from sucker. iv. Strand *a* enters the central cylinder of the first internode, first giving off two peripheral traces, *a'* : at the same level strand *b* enters the internode. ii. Strand *b* enters the central cylinder after branching (branches *b'*). (See also fig. 68.)

or, in a few cases, a single vascular strand curves upwards for a very short distance at the base of the ligule. This was also noted by Sargant and Arber, but the subsequent behaviour of the strands was not followed by them.

Transverse sections (fig. 50) examined from the root upwards show a tetrarch root stele and a scattered arrangement in the hypocotyl. Two strands proceed from the tip of the cotyledon, through the stalk, but instead of one or both turning downwards directly or indirectly towards the root, both strands turn upwards. The first node, slightly above the level of the stalk, is oblique.

Strand (*a*) approaches the central mass of vascular tissue immediately below the first internode. It splits into three ;

the median trace moves to the core of the axis, while the lateral portions ascend peripherally. The second cotyledon

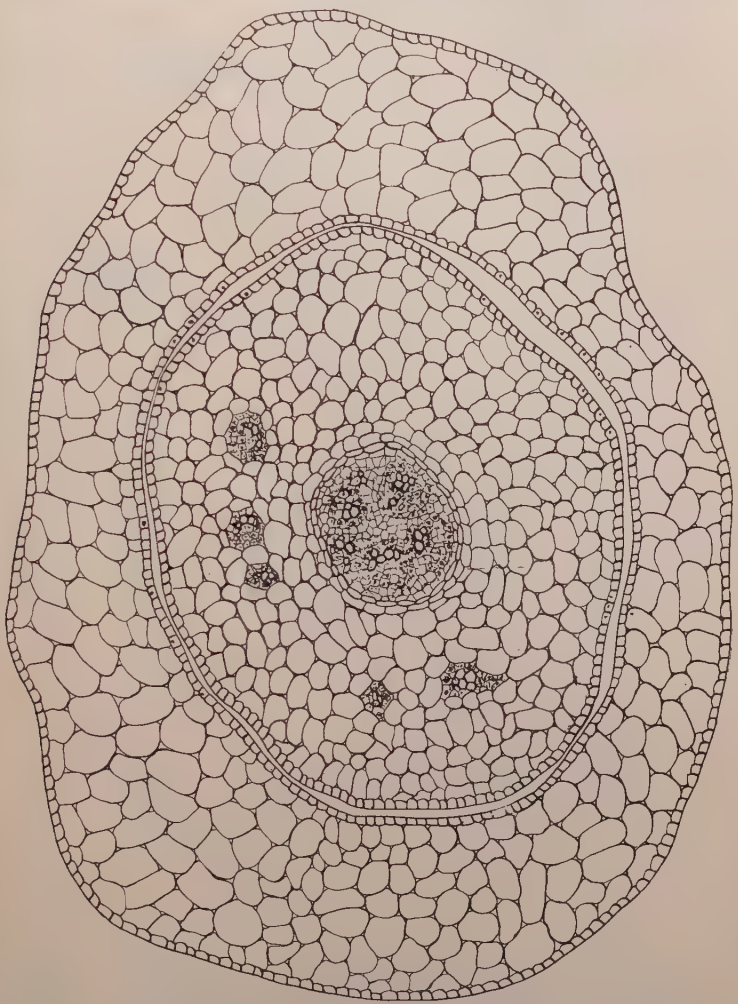

FIG. 51.—*Alpinia calcarata*. Transverse section of first internode, the cortical traces being branches of cotyledon strands. The internode is surrounded by the non-vascular ligule (× 90).

strand (*b*) also enters the plumular axis and behaves in a similar manner.

The strands of the first leaf are therefore derived solely from the cotyledonary traces, which also provide their

remaining elements for the supply of second and succeeding leaves. It can be truly stated in this instance that the cotyledon has no sheathing base.

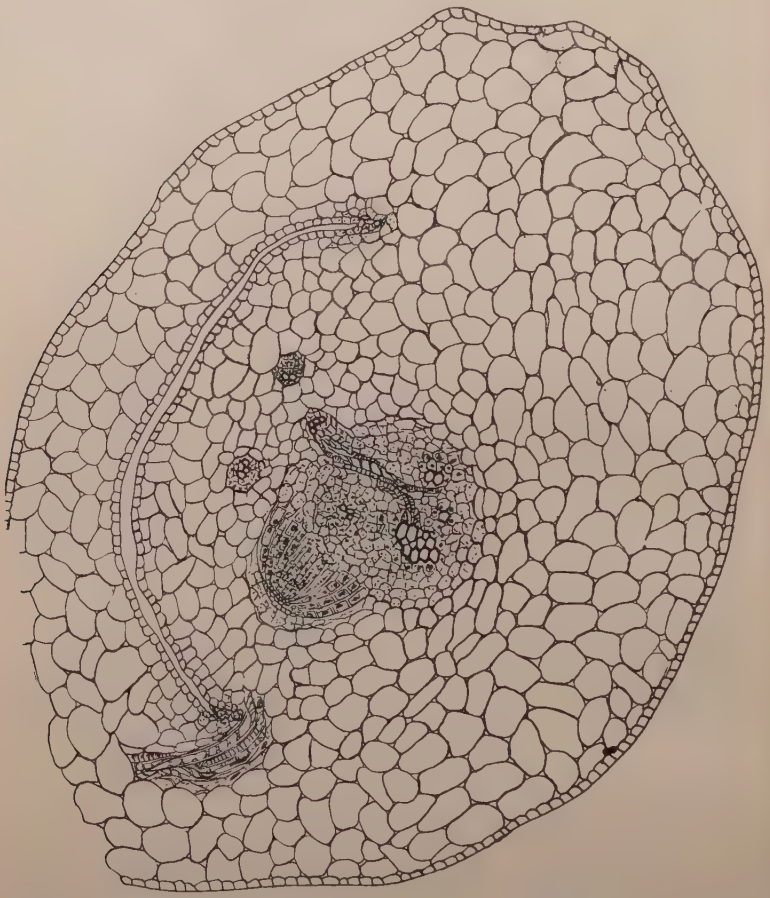

FIG. 52.—*Alpinia calcarata*. Transverse section of seedling at the level at which cotyledon strand *a* enters the central cylinder and strand *b* passes from the sucker to the internode. An adventitious root is in process of formation (× 90).

B. COSTOIDEAE.

Costus.

An account of the germination and seedling of *Costus speciosus* (fig. 53) has already been published (15). Seedlings

of *C. spicatus* and *C. afer*, subsequently examined, showed similar features. The chief interest of the genus lies not only

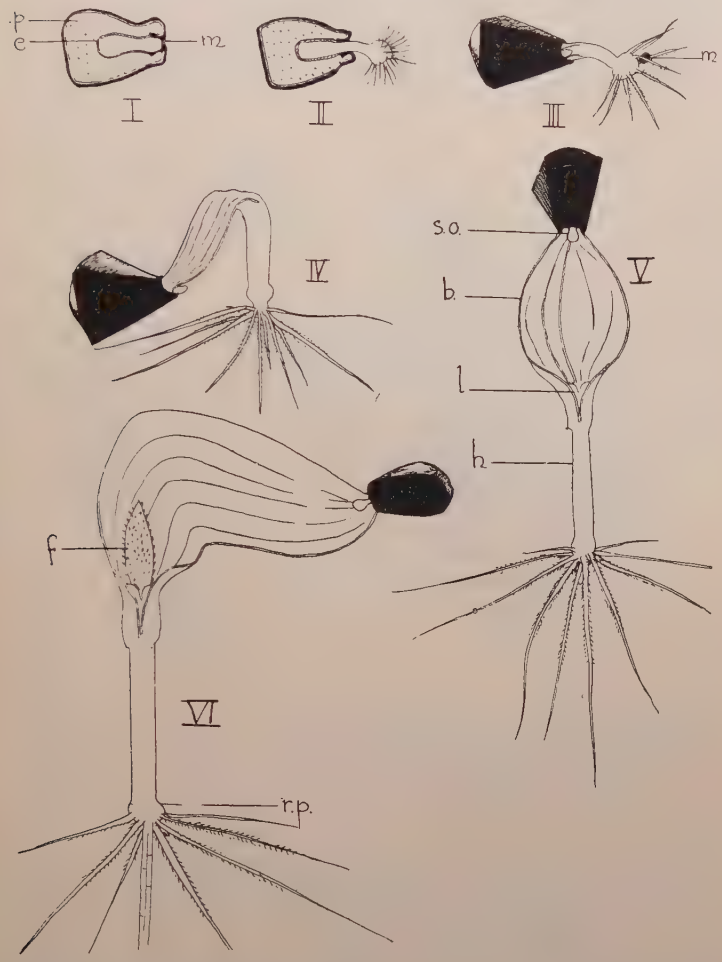

FIG. 53.—*Costus speciosus*. I. Ripe embryo in seed (×4). II–VI. Seedlings one, two, and three days, six weeks, and twelve weeks old (×4).

b=lamina of cotyledon; *f*=first leaf; *e*=endosperm; *p*=perisperm; *h*=hypocotyl; *s.o*=spherical outgrowth; *m*=germinal lid; *r.p*=root plate; *l*=ligular outgrowth.

in its wide divergence from the Zingiberoideae in external and internal seedling morphology, but in its peculiar cotyledonary anatomy (fig. 56).

The primary root never functions, but is replaced by cauline

roots arising from the base of the lengthy hypocotyl. The cotyledon tip of the seedling is cylindrical, the blade is a wide, flattened structure with highly differentiated tissues supplied by five strands (a number which later increases). In the lengthy hypocotyl the cotyledon and plumular traces behave independently of each other. At the apex of the lamina

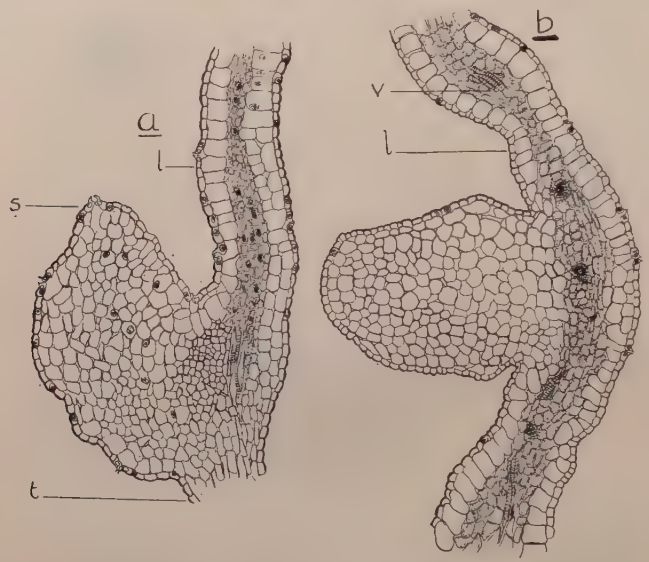

FIG. 54.—*Costus speciosus*. *a*. Median longitudinal section of cotyledon lamina of a young seedling, showing spherical outgrowth. *b*. Transverse section of same (× 40).

s = stoma ; *l* = cotyledon lamina ; *v* = vascular strand ; *t* = cotyledon sucker.

where the cotyledon tip enters the micropyle of the seed there arises a small, non-vascular, spherical outgrowth (fig. 54), while a ligular outgrowth from the base of the cotyledon lamina partially sheaths the plumule (fig. 55). Tentative suggestions have been put forward regarding the ligule and the plug at the micropyle.

Further light has been thrown on the early differentiation of the cotyledon by examination of ripe embryos of *C. speciosus* and *C. afer* from preparations by Mr. Evans (fig. 57). The cylindrical embryo (2 mm. × 0·6 mm.) has a uniform diameter except in the neighbourhood of the plumular bud, which occurs mid-way between the cotyledon tip and the root apex ;

the proportion of hypocotyl in the ripe embryo is therefore considerable. The vascular skeleton is straight. The five strong strands which are found in the solid cotyledon sucker tend to become lateral as they pass towards the base. In the zone above the plumular bud the cotyledon becomes differentiated into a solid, non-vascular, terminal core (the down-

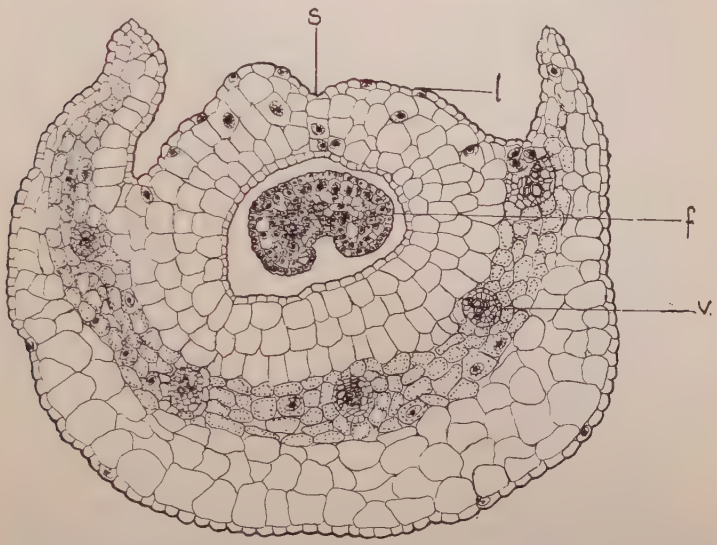

FIG. 55.—*Costus speciosus*. Transverse section towards the base of the cotyledon lamina of young seedling, showing the ligular outgrowth (×80).

f = first leaf; *l* = ligular outgrowth; *s* = region at which the upper margin of the ligular outgrowth tends to split; *v* = vascular strand.

ward prolongation of the sucker) and a lamina, lateral in origin, extending round two-thirds of the circumference of the core. The vascular strands, now increased by bifurcation of the original traces to ten, are disposed symmetrically round the lamina, which narrows towards the edges: its tissues are markedly meristematic. At germination it extends in width and length and becomes green. In the ripe embryo and seedling it never completely encircles the core, which narrows, then abruptly terminates, immediately above the plumular bud. At a level 10–20 μ lower, a ligular outgrowth appears from the inner surface of the lamina, bridging the gap between the margins (which may be regarded as an unusually wide cotyledon slit) and surrounding the plumular bud. A median

trace from the plumular meristem, surrounded by seven cotyledon strands, descends to the root apex. Thirteen or more adventitious root initials are found in the hypocotyl.

It would be extremely interesting to follow the embryology from the initial stages. As it is, the mature embryo shows

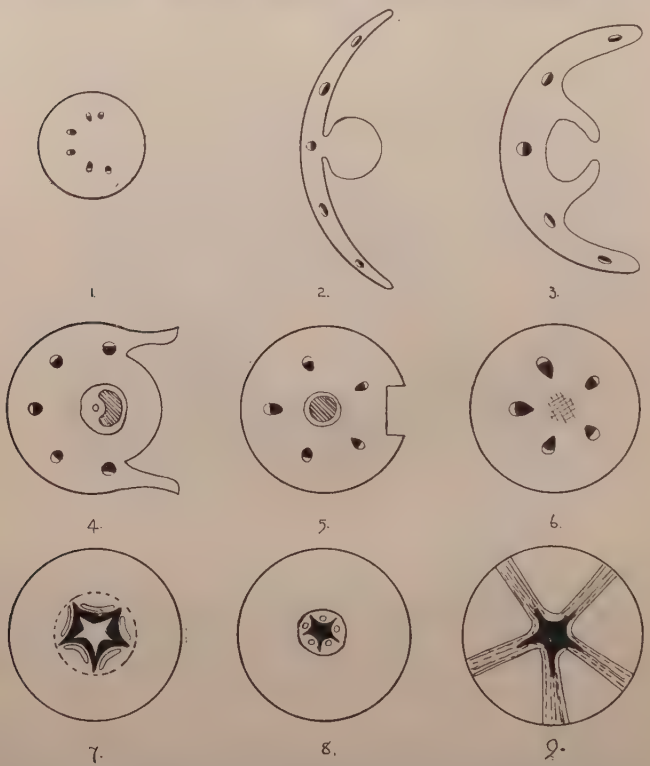

FIG. 56.—*Costus speciosus.* Transverse sections of seedling six weeks old, from the tip of the cotyledon (1) to the root plate (9).

such striking resemblances to the seedling that many points are still left obscure. It is clear that the major portion of the laminar tissue of the cotyledon is equivalent to the zone which in normal seedlings elongates to propel the primary root through the micropyle. After germination this zone provides in the common type of epigeal seedling a lamina with a cylindrical base which completely ensheathes the plumule. Such seedlings have, in marked contrast to *Costus*, weakly differentiated plumules. In *Costus* the plumule is not only

precocious, but its position in the mature embryo is terminal, since it lies in direct alignment with the core of the sucker and with the hypocotyl and root apex. The blade of the cotyledon in the seedling is a lateral structure both in its origin and in its relation to the plumule. In view of this,

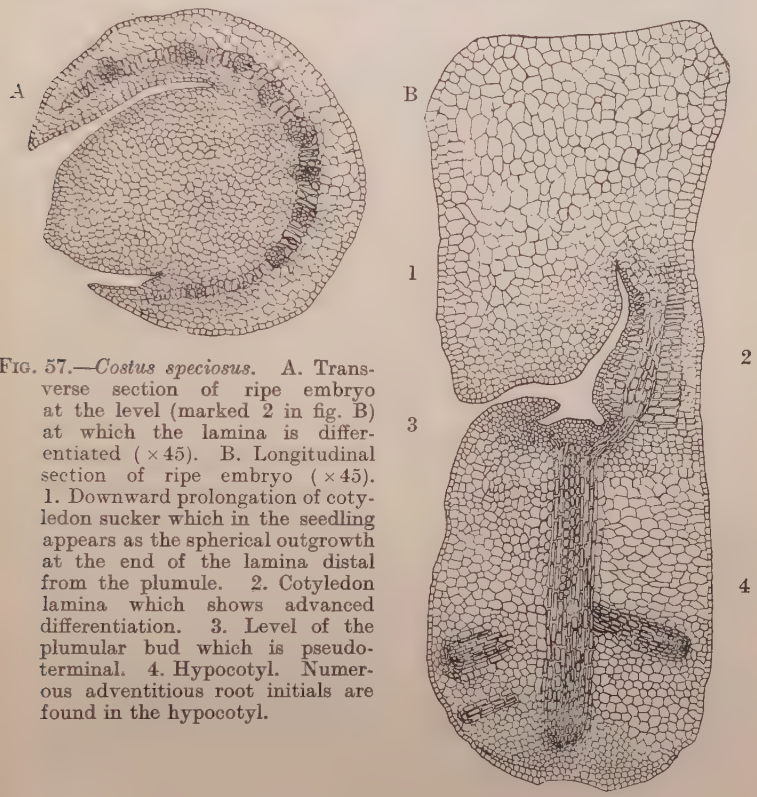

FIG. 57.—*Costus speciosus.* A. Transverse section of ripe embryo at the level (marked 2 in fig. B) at which the lamina is differentiated (×45). B. Longitudinal section of ripe embryo (×45). 1. Downward prolongation of cotyledon sucker which in the seedling appears as the spherical outgrowth at the end of the lamina distal from the plumule. 2. Cotyledon lamina which shows advanced differentiation. 3. Level of the plumular bud which is pseudoterminal. 4. Hypocotyl. Numerous adventitious root initials are found in the hypocotyl.

the ligular outgrowth at its base finds a more complete interpretation: its morphological significance is similar to that of the ligule of the ordinary foliage leaf, lateral to the plumular bud which it protects, or to the stem which it ensheathes.

The prolongation of the solid sucker into a plug which on germination is withdrawn from the seed is still unique in Monocotyledons. Its volume does not increase after germination, and it might therefore be viewed as belonging to the tissue of the suctorial tip, which does not increase by cell division. It seems that evolution has affected differentiation in the

embryo to such an extent that the origin of " laminar " tissue has been increasingly extended until sucker tissue, originally undifferentiated, has become involved. The differentiation into lamina at the base of the sucker tissue has, however, been incomplete, and the core has remained as a vestige which is withdrawn from the seed by the meristematic lamina, which was separated off from it. The retention of the core has incidentally two possible advantages. It helps to keep the embryo straight by preventing collapse of the laminar tissue, and after germination it acts as a stopper by plugging the germinal aperture.

Research on seedlings of Costoideae has hitherto been almost entirely neglected. Gatin (55) figured a seedling of *Tapeinochilos pungens* Miq. which resembles the seedling of *Costus* in external morphology. Whether or not the plug of cotyledon tissue closes the circular aperture in the seed coat cannot be determined from the sketch.

Literature on the Seedlings of the Scitamineae.

Lubbock's account (97) of Marantaceae is merely a short discussion of the dehiscence of the fruit. Humphrey (82) refers to the curved embryo of *Thalia*. Information regarding the initial stages in the life-history of Marantaceae is almost entirely lacking.

In Musaceae, Humphrey deals with the seed of *Musa*, *Strelitzia* in which there is no functional perisperm, and *Heliconia* which has no micropylar collar. Gatin (53) remarked on the poor differentiation of the embryo of the latter ; he also studied *Ravenala*, *Strelitzia*, and *Musa*. In the embryo of *Musa* the cotyledon has a somewhat unusual form. Gatin correlated the morphology of germination of Cannaceae and Musaceae with the curvature of the axis in the embryo, and emphasised the endogeny of the radicle in the Scitamineae. He noted that since the strands of the cotyledon form at its base an arc which may have a plane of symmetry through a median bundle or through two groups of identical bundles, these families give no support to Sargant's double-bundle theory (119–122).

Summary.

The grouping is somewhat unsatisfactory, since the term rhizome is applied to such widely differing organs as the thin, creeping underground stem of some species of *Trillium*, and the bulky perennating bodies of many of the garden varieties of *Iris*. The development of the rhizome is frequently not obvious until the plant is far beyond the seedling stage. There is accordingly no apparent difference between the seedling of an annual and of a perennial Commelinaceous plant, save possibly the more rapid growth of the former. It was scarcely to be expected that this group would show the uniformity found in others in which the perennating organ varied little in its form. Possibly on this account family resemblances are strongly marked. The Zingiberaceae and Commelinaceae, for instance, form complete units apart from considerations of habit.

There are no marked divergences from the average size of seed except in *Canna* and *Hemerocallis*, genera having numerous cotyledon strands and root poles.

The precise mechanism by which the elongating embryo on germination pushes out a micropylar lid is seen in Commelinaceae, Cannaceae, and certain of the Zingiberaceae and Liliaceae.

Germination is hypogeal, and the cotyledon ligulate in Zingiberoideae, Commelinaceae, and Cannaceae. The Costoideae discussed have an epigeal cotyledon. All types of germination are found in Iridaceae and Liliaceae. In the Liliaceous seedlings examined the ligulate type of cotyledon predominates, whereas the majority of Iridaceae have the hypogeal, non-ligulate cotyledon. Seedlings in the same tribe—for example, the Medeoleae and Hemerocalleae—tend to have the same type of cotyledon. It is interesting to note that *Bowiea* and *Chlorophytum*, belonging to the same tribe though differing in the habit of the adult, present different types of seedling morphology.

In seedlings having a hypogeal and in particular a ligulate cotyledon, plumular development is strong, and growth of the early leaves rapid. The importance of the plumule is indicated by its differentiation in the embryo. *Heliconia* (Musaceae) is conspicuous for the retardation in plumular

development (53), while the advanced condition of the plumule in the embryo of *Canna* is remarkable. The first foliar organ in Cannaceae and Zingiberaceae may be a scale leaf, the mature type of leaf frequently not appearing until the third leaf expands.

The cotyledon anatomy within a family is in some degree constant.

1. In Liliaceae the double bundle or its equivalent is the common vascular system. The Medeoleae are exceptional in having a laminate cotyledon possessing a mid-rib and two lateral strands in the stalk and base of the cotyledon, in relation possibly to its value as the only photosynthetic organ for a season. The cotyledonary strands of *Hemerocallis* vary from four to seven in number ; even in a species the number is not constant.
2. The cotyledon of Iridaceae possesses a double bundle, or a single bundle becoming double towards the base, or a single bundle.
3. Seedlings of Commelinaceae have two strands following an almost parallel course throughout the greater part of the cotyledon.
4. The Zingiberoideae have two strands in the cotyledon :—

   (*a*) Both strands may enter the ligule (*Roscoea*), though one may descend almost immediately.

   (*b*) One strand may ascend a short distance in the ligule, while the other directly enters the first internode (*Hedychium*).

   (*c*) Both strands may directly enter the plumular axis (*Alpinia*).

   These are not three distinct types of anatomy, but variations on a fundamental type (fig. 68). In each example cited, the cotyledon traces enter the first internode and supply the plumular bud.
5. The large number of strands in *Costus* (Costoideae) affords a marked contrast to the constancy of the two strands in the other sub-family.
6. The Cannaceae may have from five to twelve strands in the cotyledon sheath. The sheath is taken as the most satisfactory region for comparison, since large numbers are found in the cotyledon tip owing to ramifications.

The development of the primary root is variable. In Commelinaceae the primary root is ephemeral, being replaced by cauline roots, which originate with beautiful symmetry and precision. It is markedly endogenous in the Scitamineae. It is suppressed in Cannaceae, although its vascular tissue is differentiated in the embryo, and the Zingiberaceae dispense with the primary root from the first or after a few weeks. The need for a copious supply of adventitious roots is then obvious ; their initials are well defined in the embryo.

Root anatomy is, on the whole, simple.

(*a*) Two, three, or four protoxylem groups are common in Liliaceae. *Hemerocallis* with a pentarch, hexarch, or heptarch root is again exceptional.

(*b*) The stele in Iridaceae varies from diarchy to tetrarchy.

(*c*) Tetrarchy or triarchy is found in general in Commelinaceae.

(*d*) The primary root stele of Cannaceae is of such a nature as to be indeterminable.

(*e*) Diarch and tetrarch roots are found in Zingiberoideae.

A distinct hypocotylar region is not always found. When the cotyledon is ligulate, it is usually absent. In the Commelinaceae its development is pronounced. The hypocotyl has root structure in certain Liliaceae, for example, *Chlorophytum*. The swollen hypocotyl in the Medeoleae recalls the tuberous hypocotyls in the previous group and has a comparable vascular structure.

Plants showing a Climbing Habit.

Liliaceae.

A.—Non-woody type.

Tribe Uvularieae—*Gloriosa* sp.

A berry, 6·0 mm. in diameter, contains a single seed. The embryo, a straight narrow body, 2 mm. long, with an asymmetric vascular skeleton, is embedded in hard endosperm.

Germination is Type C (fig. 58). The cotyledon consists of a well-developed club-shaped tip, constricted at the micropyle, a very short, stout stalk ($\frac{1}{2}$ mm. in length), and a ligule (3–10 mm. long) which continues for some days to elongate with the first leaf and is provided with a slit for its emergence.

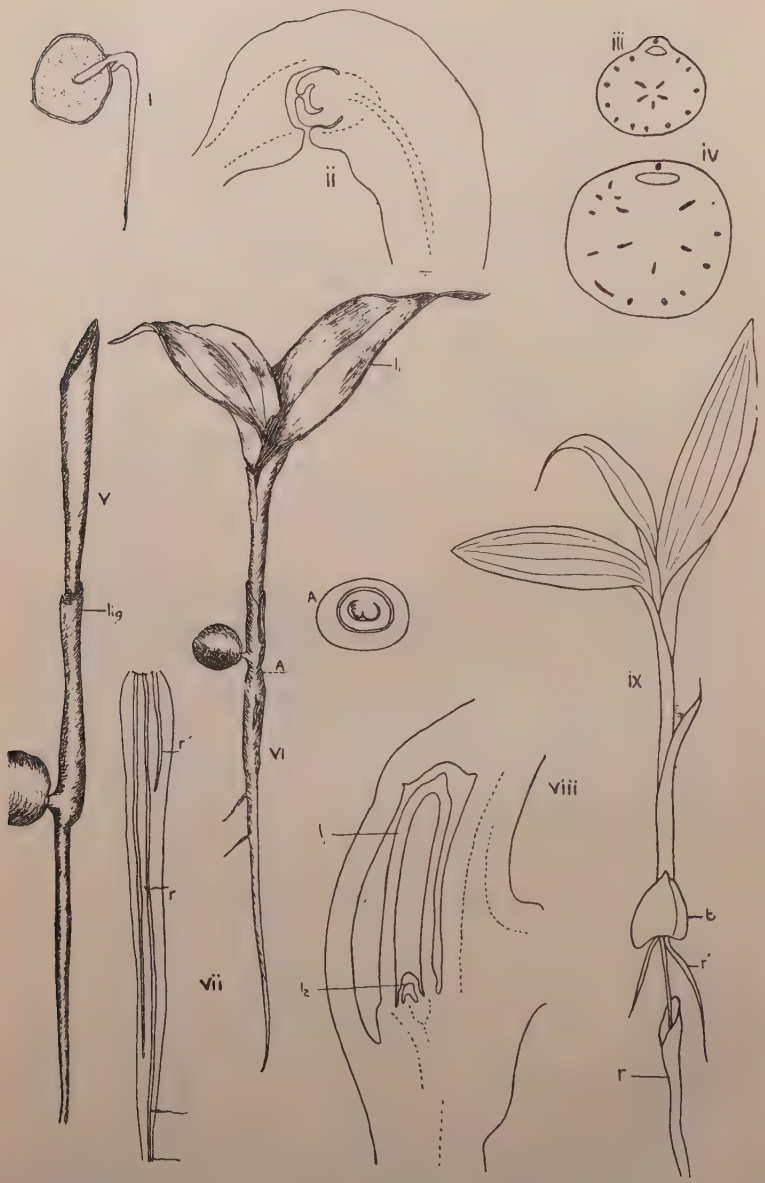

FIG. 58.—*Gloriosa* sp. i. Seedling a few days old: the seed has been cut to show the cotyledon sucker in endosperm (× 3). ii. Longitudinal section of part of seedling figured in i, showing the plumular bud (× 20). iii–iv. Sections towards the apex and middle of the tuber of seedling figured in ix; the mid-rib of the third leaf passes down a ridge outside a hollow which is the prolonged axil of the third leaf (× 6). v. Seedling

The fleshy sheathing base of the cotyledon is approximately $1\frac{1}{2}$ mm. long. The plumule is massive in comparison with the whole seedling. The first leaf has a mid-rib and four pairs of lateral strands. There is practically no hypocotyl. The primary root is 10 mm. long when the plumule is only about to emerge from the seed. Its remarkable growth in width and length emphasises its importance. The piliferous layer appears to be absent, the root having a succulent, transparent appearance. When the first leaf is free (then approximately 7 mm. high), the primary root produces numerous lateral rootlets at right angles to the stele, though none at this stage break through the root epidermis. The first adventitious root is then making its way through the cortex.

Anatomy.—Four types will be described.

(*a*) Four well-defined strands are arranged in pairs in the cotyledon tip. Below the stalk two double bundles pass into the sheath, and at slightly different levels join the plumular meristem which consists of three and, lower, two masses. After union with the cotyledon strands there are six xylem traces, which, by the union of a pair, reduce to five; they arrange themselves in two crescents (each formed from a pair) joined by the fifth. The protoxylem moves outwards. Splitting of fifth uniting xylem band into two more peripheral strips results in a hollow rectangular patch of xylem. The primary root is diarch.

(*b*) Three strands are found in the cotyledon stalk. The central strand proceeds vertically for a short distance, then bends sharply downwards through the sheath. The lateral traces, on leaving the stalk, bifurcate. A branch of each

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two weeks old in which the first leaf has emerged through the ligule ($\times 4$). vi. Seedling five weeks old ($\times 2$); the ligule has been split by the growing leaf bases, and the plumular bud is to be found at the level marked A; the epidermal tissues of the primary root have begun to rupture (see fig. 60). vii. A primary root at this stage, with the epidermis slit to show the growth of two adventitious roots parallel to the stele of the primary root, which is producing lateral rootlets towards the tip ($\times 2$). viii. Longitudinal section of seedling before the first leaf pierces the ligule ($\times 16$). ix. Young plant which has become tuberous. The tuber is protected by the bases of the first and second leaves. The ridge on the tuber marks the superficial passage of a strand from the third leaf. The cortex and epidermis of the primary root are sloughing off, and the third and succeeding leaves are above ground ($\times \frac{3}{2}$).

l_1, l_2=first and second leaves; *lig*=ligule; r=primary root; r'=adventitious root; t=tuber.

continues to the tip of the ligule, and turns downwards parallel and very close to the upward strand (giving the appearance of double bundles). At the bottom of the ligule each branch is joined by the remainder of the strand which produced it,

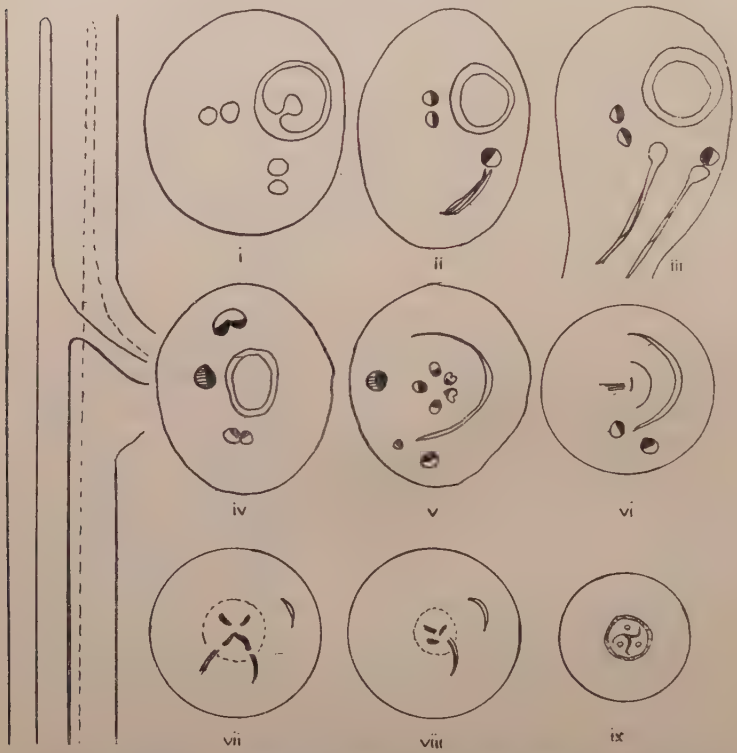

Fig. 59.—*Gloriosa* sp. Transverse sections of young seedling from a level above the cotyledon stalk (i) through the stalk region (ii–iii) and sheathing base (iv–vi) to the hypocotyl (vii–viii) and primary root (ix). The course of the cotyledon strands is indicated diagrammatically on the left. (Anatomy described as Type C.)

and below the stalk becomes a double bundle. (The central strand is single.) The strands fuse in turn with the plumular meristem (derived from five first-leaf bundles). Three separate xylem rays, so formed, unite and give rise to a triarch root.

(*c*) A central and two lateral strands proceed from cotyledon stalk (fig. 59). The lateral strands ascend the ligule, separate at the apex, and proceed to the base of the cotyledon, one entering the stele before the other. They remain single throughout.

The central strand in the cotyledon stalk is single ; it does not enter the ligule, but descends through 230 μ, entering the stele after the first and with the second lateral strand. The root is triarch.

(*d*) The fourth type is a compromise between (*b*) and (*c*). The central strand is double ; one lateral strand bifurcates ; a branch enters the ligule, descends, and unites with the trace from which it sprang. The other lateral strand remains single. The root is triarch, with an isolated element representing a fourth arm of xylem.

Further Development of the Seedling.—After a month the region of the cotyledon sheath and upper part of the root increases in girth. A longitudinal rupture occurs in the root epidermis and cotyledon sheath (fig. 58, vi). Sections taken below the constriction, which in young seedlings marked the upper limit of the root, show that the root epidermis no longer protects the cortex and stele of a root, but surrounds the base of the first and succeeding leaves. The upper limit of the primary root stele is found 2 or 3 mm. lower than its original level, and the primary root, which has a semi-transparent epidermis and cortex, appears to have three steles instead of one. When the loose epidermis is peeled off, two adventitious roots are seen to have arisen at the base of the stem. Instead of making their way outwards, they have grown through the cortex of the primary root parallel to the central cylinder. Each behaves independently of the other, and of the primary root stele, which, towards its tip, produces numerous horizontal rootlets. The stele of the adventitious roots has six peripheral poles. The change of position of the primary root seems to be caused by the adventitious pull roots, which drag the plumular axis downwards through a hollow cylinder formed by the disintegration of the root cortex. The exact manner in which the vascular cylinder of the primary root accommodates itself to this change, and the share it takes in pulling down the plumular axis, has not yet been investigated.

The Tuber of Gloriosa.—The preparation for tuber formation is made in the first month. In the present study plants up to eight months old were examined. At this stage the three or four aerial leaves were without tendrils. The epidermis of the primary root had sloughed off, although fragments adhered to the lower part of the roots, which arose from a

subterranean, pear-shaped, tuberous body. The latter was covered by the bases of the first and second foliage leaves, which had nine vascular strands. The naked tuber, from

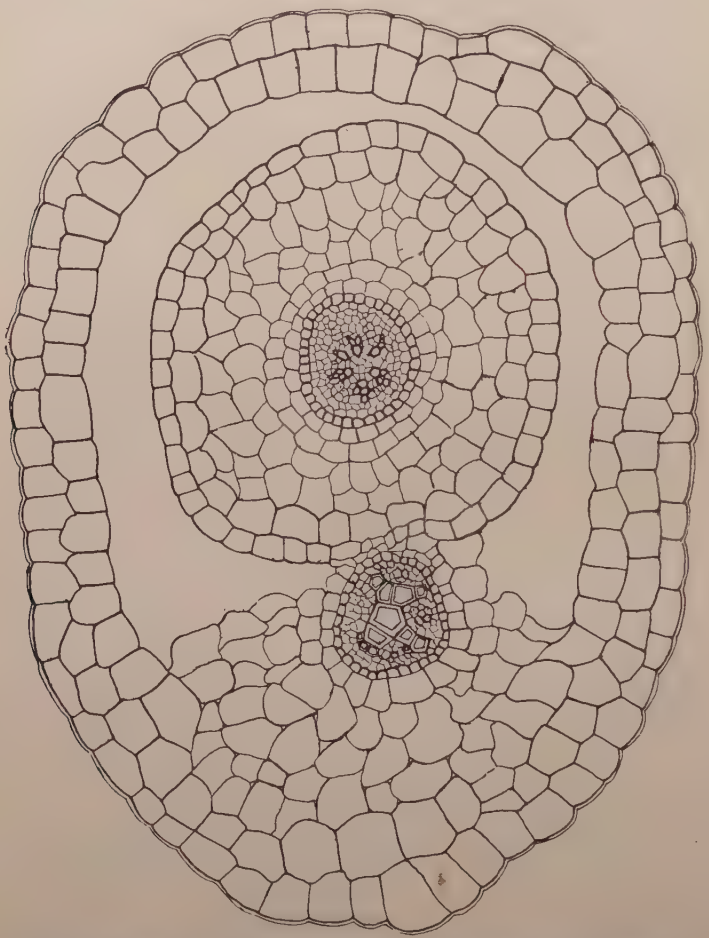

FIG. 60.—*Gloriosa* sp. Transverse section of primary root in which a hexarch adventitious root has pierced the cortex of the primary root, which has a tetrarch stele (× 70).

the top of which arose the base of the third leaf, was smooth. Its strands were peripherally and centrally arranged. The downward continuation of the mid-rib of the third leaf proceeded near the surface from the apex to the base of the tuber, producing the appearance of a ridge.

The tuber is the result of accumulation of starch by the lower half of the third internode. Hypocotyl and the first two internodes take no part in its formation, though the bases of the first and second leaves provide a tunic for it. The bud in the axil of the first leaf aborts. The " bud " of the second leaf axil ought to occur on the dorsal side towards the base of the tuber, the other on the ventral side half-way between the apex and base. Both are replaced by meristem, the activity of which leads to extension of the tuber. Queva (108) describes the (*a*) type of anatomy of the seedling, the unusual root development, and the origin of the tuber. He believes that, although tuberisation is absent in the embryo, the seedling shows several significant features—for example, the long sheath of the first two leaves, the shortness of the first two internodes, lack of buds in the axil of the cotyledon and the first two leaves, and presence of the " axillary canal " (fig. 58, iii, iv) which prolongs the axil of the third leaf close to the second node.

B.—WOODY TYPE.

Tribe Luzuriageae—*Lapageria rosea.*

The plant is a high-climbing shrub having coriaceous, heart-shaped leaves with 3–5 nerved reticulate venation. The barrel-shaped seed is 4·5 mm. long, covered with a thin, transparent testa. The endosperm is extremely hard. Germination is Type B (fig. 61). A swelling a little above the very marked root-cap indicates the position of the plumule. Development, once begun, is rapid. The cotyledon consists of a club-shaped suctorial tip occupying half the seed, a short, thick stalk, and a sheathing base which arches to form a low, open upper sheath. The first and second leaves, or the first leaf alone, is rudimentary. The third leaf reproduces the shape and venation of the adult plant and has a strong mid-rib flanked by two pairs of lateral strands which fuse at the base of the lamina. The internodes are long. A large bud may occupy the axil between cotyledon and first leaf. The primary root is strong and persistent, tapering towards the tip. In the initial stages its length increases at the same pace as the shoot.

Anatomy.—Three equidistant strands, the central being a double bundle, run through the cotyledon tip and stalk.

The bicollateral bundles of the stem have very large xylem vessels and a good proportion of phloem. The inner ring of

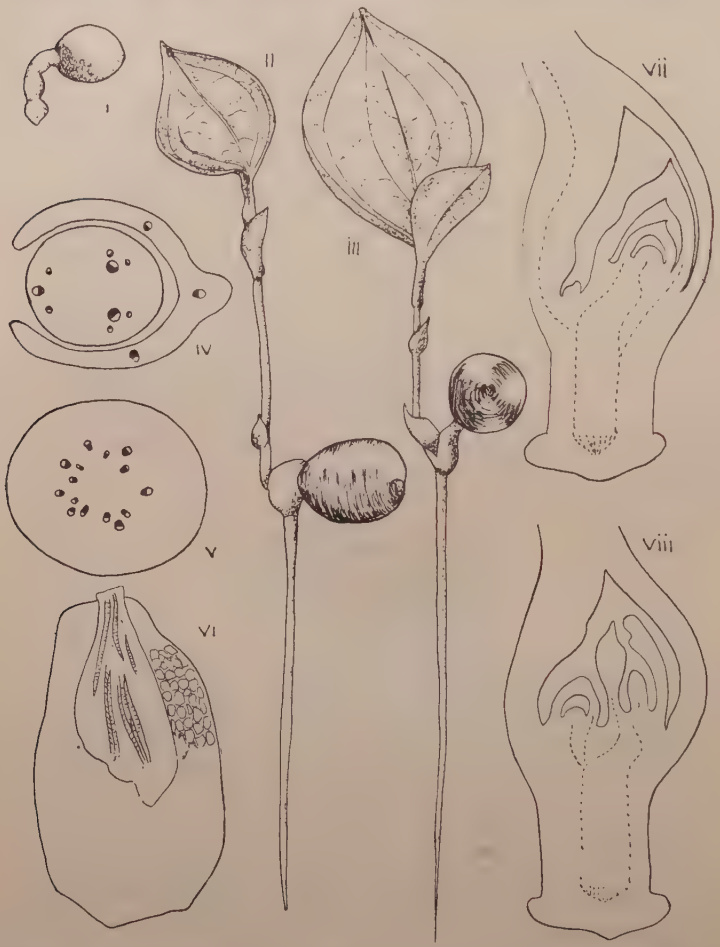

Fig. 61.—*Lapageria rosea*. i. Seedling a few days old (× 2). ii. Seedling with the third leaf expanded (× 3). iii. Seedling of the same age, showing the development of a bud in the axil of the cotyledon (× 3). iv. Transverse section of base of first scale leaf and second internode (× 25). v. Transverse section of first internode (× 25). vi. Longitudinal section through seed and cotyledon sucker (× 10). vii. Median longitudinal section of seedling figured in i (× 20). viii. Tangential longitudinal section of same seedling, showing a bud in the axil of the cotyledon and its vascular supply (× 20).

large strands surrounded by small peripheral traces (fig. 61) recall the dicotyledonous arrangement. At the base of the

stem the cotyledon traces are inserted on those of the plumule, forming a closed woody ring enclosing a large pith. Phloem lies outside the xylem. Lower, the ring disintegrates to give a typical root stele, with seven or eight xylem poles. The bud in the axil of the cotyledon is supplied by a strong vascular strand passing independently to the hypocotyl.

Tribe Asparageae—*Asparagus*.

With the exception of *A. racemosus* and *A. madagascariensis*, the embryo and germination of the species for which seedlings were obtained had already been described by Evans (44).

Asparagus racemosus.—The embryo is similar to that of other species of *Asparagus*, being long, cylindrical, and narrow, lying in extremely hard endosperm. The short, thick primary root emerges by pushing out a micropylar lid. Like that of *Lapageria*, it is protected by a strong root-cap. In the first days after germination the plumular bud is completely covered by the overlapping margins of the cotyledon slit (fig. 62). When it emerges it consists of leaf primordia and a stem apex. The first leaf, a kataphyll, remains partially enclosed by the short, wide cotyledon sheath.

In the species examined by Evans (44) the first internode never elongates, and this observation is true also of the second internode in two species whose second leaf is also a kataphyll within the cotyledon sheath. The second and succeeding internodes of *A. racemosus* are long, and the early leaves mere scales. The primary root increases in girth and becomes contractile. At the end of the first month a contractile cauline root and three or four purely nutritive roots supplement the primary root, which is hexarch. Above the kataphyll the stem shows a ring of six strong vascular strands surrounded by a cylinder of sclerenchyma. A mid-rib and a pair of weaker lateral strands proceed through the youngest internode.

Asparagus madagascariensis (fig. 62, xiii).—One root of this plant had swollen to remarkable dimensions: its stele had sixteen xylem poles peripherally arranged. A second thin root of equal length was hexarch. In all probability the latter was the primary root, although the swelling of the primary root of *Asparagus* seedlings to large dimensions has been recorded (44).

Anatomy of the Seedling in General.—Even in a species Evans (44) found a lack of uniformity in the cotyledon anatomy of the embryo, the number of strands varying from three to

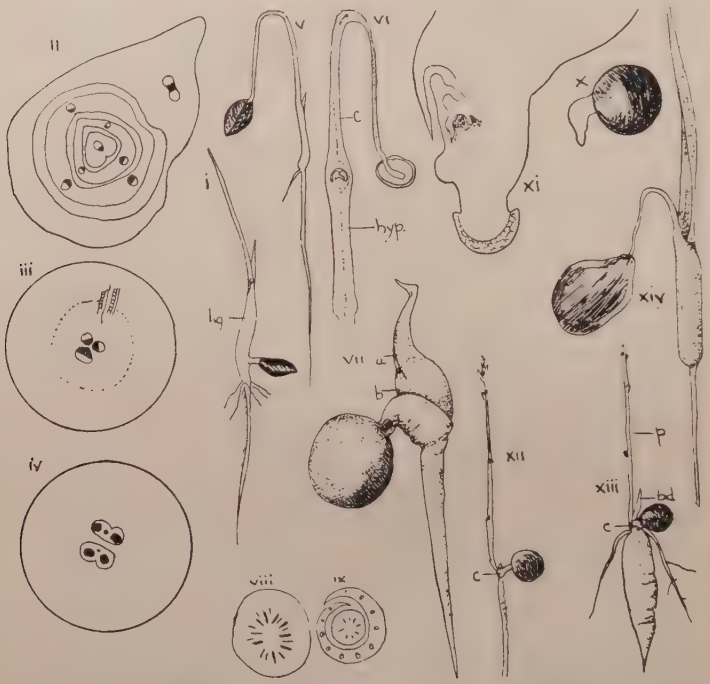

Fig. 62.—i–iv. *Astelia* sp. i. Seedling a week old (×2). ii. Transverse section of cotyledon ligule surrounding the first leaves. iii. Upper limit of hypocotyl. iv. Hypocotyl. v. *Cordyline Banksii*: young seedling, showing the first leaf emerging through the cotyledon slit (×3). vi. Longitudinal section of younger seedling (×4). vii. *Dracaena Draco*: young seedling (×2). viii. Transverse section through level marked *b* in vii (first internode) (×2). ix. Transverse section through level marked *a* in vii (base of first leaf and second internode) (×2). x–xii. *Asparagus racemosus*. x. Seedling two days old (×2). xi. Longitudinal section of seedling figured in x; there is a prominent root cap (×25). xii. Seedling a few weeks old: the young leaves are reduced to mere scales (actual size). xiii. Seedling of *Asparagus madagascariensis*, showing bud in the axil of the cotyledon and storage in the root (actual size). xiv. Seedling of *Yucca Whipplei* (×2).

bd = bud; *c* = cotyledon; *hyp* = hypocotyl; *lig* = ligule; *p* = plumular axis.

five. Sargant (120) notes three strands in the cotyledon of the seedling and a variation in the primary root stele from tetrarchy to heptarchy, seedlings with rhizome buds within the cotyledon sheath providing the extreme cases.

Apart from the genera discussed, *Littonia* (108) and *Smilax* (44) are apparently the only Monocotyledonous climbers of which a record of the seedling morphology has been made.

Summary.

The primary root is remarkable for its length and the development of its central cylinder. Lateral roots are infrequent at early stages. *Gloriosa* affords an unusual instance of augmentation of the primary root without secondary thickening. The vascular anatomy of the root is in no way remarkable, though Queva (108) emphasises the fact that the primary root stele of *Gloriosa* at the upper limit is diarch, but lower tetrarch.

Germination is hypogeal. The cotyledon of *Gloriosa* is markedly ligulate and shows a variability in anatomy which may find an explanation in the final discussion (p. 183).

Where the hypocotyl is a distinct region, plumular and cotyledonary strands run parallel through most of its length. According to Sargant (120) their behaviour in *Asparagus* is similar to that of hypocotylar strands in arborescents.

The rapidly developing plumule dominates the young seedling. In *Gloriosa* which produces a tuber, and *Asparagus* which is rhizomatous, the first two internodes are short. The stem structure is similar to that of a Dicotyledon, doubtless because the mechanical requirements of Monocotyledonous and Dicotyledonous climbers are akin. The presence of large vessels, buttressed by sclerenchyma and bicollaterally arranged, indicates to some extent the climbing habit.

The early leaves do not resemble the adult leaf. They may take the form of kataphylls (*Asparagus* and *Smilax*) or be very rudimentary (*Lapageria*). In *Gloriosa* the early leaves have no tendrils.

As Queva (108) and Evans (44) have pointed out, it is possible, chiefly from an examination of the plumular meristem and its development in the young seedlings, to make some reconstruction of the adult form of the plant.

Plants having an Arborescent or Shrubby Habit.

Liliaceae.

Tribe Dracaeneae—*Cordyline Banksii.*

The endosperm is absorbed rapidly from the seed, which is 2 mm. in length and spherical or ovoid in shape. Germination is epigeal (fig. 62, v, vi). Development proceeds at the normal rate for seedlings of the family. The cotyledon is cylindrical, with a uniform cross-section throughout most of its length, and is traversed by a double bundle. The hypocotyl, which may equal the cotyledon in length, has a strongly cutinised epidermis, wide cortex, and a triarch or tetrarch stele with an endodermal sheath. It is thicker than the primary root and, save in colour, is indistinguishable externally from the cotyledon sheath. As the primary root ages, the cortex dries and withers, but the triarch stele, sheathed in a very thick sclerenchymatous layer, still functions. From the first week a single cauline root having a polyarch stele assists the primary root. Anatomically, the species agrees with *C. australis* (described by Sargant), which has a transition according to van Tieghem's Type 1. The embryos of the latter species, *C. cannaefolia*, and *C. angustifolia* were examined. The embryo of *C. australis* is curved, though the vascular system is symmetrical. In each species the plumule is poorly differentiated, and there are two cotyledon strands.

Astelia sp.

The seed is similar to that of *Cordyline*. Germination is Type C (fig. 62, i). The sheathing base of the cotyledon is 1–2 mm. in length. The ligule is variable in length and may be three or four times as long as the sheathing base, or barely as long. A short stalk connects it with the suctorial tip, which at germination almost fills the seed. The first leaf, which is linear lanceolate, has a mid-rib and a pair of lateral strands. Internodes are exceedingly short. The long, tapering primary root at an early stage produces rootlets and is assisted by a cauline root. The adult plant has a short, thick rhizome.

Anatomy.—The double bundle of the cotyledon proceeds

from the tip, does not pass into the ligule, but joins the plumular traces at the base of the sheath when they have been reduced to three. Plumular and cotyledonary strands run parallel through the hypocotyl, which is comparatively short. A solid mass of xylem occupies the bulk of the stele at the upper limit of the primary root. There are four phloem groups. Lower, the root stele becomes typically triarch.

Longitudinal sections of *A. Cunninghami* show at the most a slight upward prolongation of the sheathing base of the cotyledon : a distinct ligule is not perceptible.

Dracaena.

Dracaena Draco.—The seed is spherical (diameter 8 mm.). The embryo is a cylindrical massive body (4 mm. × 1 mm.) in which the plumular bud is represented by an undifferentiated mass of tissue (fig. 72). The thin, longitudinal cotyledon slit does not expose the bud in the embryo. Five main strands proceed through the sucker, reducing to four in the hypocotyl. The root stele in the embryo is solenostelic.

Germination is Type B (fig. 62). The suctorial tip half fills the seed. The powerful development of the first internode gives the young seedling a tuberous appearance. The primary root is exceedingly strong. Sargant (120) has described the anatomy, referring the transition to Type I. The writer found nine strands in the cotyledon sheath and fourteen poles in the primary root.

Dracaena cinnabari.—The embryo is only half the size of that of *D. Draco.* In the upper part of the cotyledon sucker fifteen to seventeen vascular strands are peripherally arranged. They reduce to six massive bundles, then five, above the plumular bud. The undifferentiated plumule contributes little or nothing to the vascular symmetry. In the hypocotyl the vascular strands form a closed ring in which seven traces are distinguishable.

Dracaena Godseffiana has an embryo with the dimensions of that of *D. cinnabari.* Half the embryo consists of hypocotyl. There are eleven strands in the cotyledon sucker, reducing to seven at the base of the cotyledon.

Yucca.

Yucca angustifolia.—The cotyledon of the seedling has two main and two subsidiary strands. They enter the hypocotyl as two bundles together with the three traces which supply the plumular bud and first leaf (which has a mid-rib and two pairs of lateral strands). The five strands are parallel to each other through the comparatively lengthy hypocotyl. With little further re-arrangement a pentarch root stele is formed. *Y. Whipplei* has a similar structure (fig. 62). Its first leaf has eight or nine strands. The cotyledon strands show cambial activity.

Sargant (120) found that in *Y. aloifolia* and *Y. gloriosa* four cotyledon and three plumule strands proceed through the hypocotyl. *Y. arborescens*, which she also examined, possesses six or seven main and four subsidiary cotyledon strands, and the primary root is heptarch or octarch.

Nolina recurvata.

The anatomy follows the same plan. There are four cotyledon strands. In *N. Parryi* there are only three cotyledonary strands.

Tribe Hemerocalleae—*Kniphofia Northiae.*

The species is figured (4) as having a stem which shows secondary thickening, and thirty or forty leaves rising in close succession towards its apex.

Germination is of the *Astelia* type. Anatomically the seedling shows no peculiar features. There are two cotyledon strands, one of which enters the ligule, ascends to the tip, and, after bending sharply, descends to the base of the sheath. The hypocotyl, which is between 1 and 2 mm. in length, shows some characteristics of the root, having, for example, an endodermal sheath. The primary root is pentarch.

Palmae.

Little remains to add to the comprehensive work of Gatin (52) on the embryo and germination of the Palmae, which involves

a description of thirty-three genera and fifty-eight species. A brief account will be given of seedlings not described by Gatin and examined in the present investigation.

Cocos capitata.

Germination is Type C, the species thus agreeing with *C. australis* and *C. campestris* but not with *C. plumosa* (species described by Gatin). The plumule is markedly differentiated at germination. For anatomy, see fig. 63, xii–xv.

Chamaedorea Sartorii.

The seed is ovoid and 1 cm. in length. Germination is Type C (fig. 63). The tip of the cotyledon is spherical and traversed by fifteen peripheral strands composed mainly of phloem. There are four strands in the ligule and six in the sheathing base of the cotyledon. At an early stage the persistent, tapering root, which has fifteen xylem poles in the stele, produces lateral roots.

Latania Commersonii.

Gatin figures only the initial stage of germination. The seedling produced its first and second leaves nearly a year after sowing, but germination doubtless took place many months earlier. Germination is Type B (fig. 63). The nut-like seed, flat on one side and convex on the other, was 3 cm. long and was completely filled by the spongy suctorial tip of the cotyledon which was supplied by thirty-eight peripheral strands. The cylindrical stalk emerged, as in other seedlings, by a spherical aperture bordered by a brown and an outer white collar. Eighteen traces passed through the stalk, which was 3 cm. in length. The cotyledon sheath was 5 cm., and the root, which was woody and 10 cm. long, had given rise to numerous stout lateral roots. The first leaf has eight main and twelve subsidiary strands.

Areca sapida.

Gatin describes the type of embryo but not the germination. Germination is hypogeal. The cotyledon is ligulate (fig. 63).

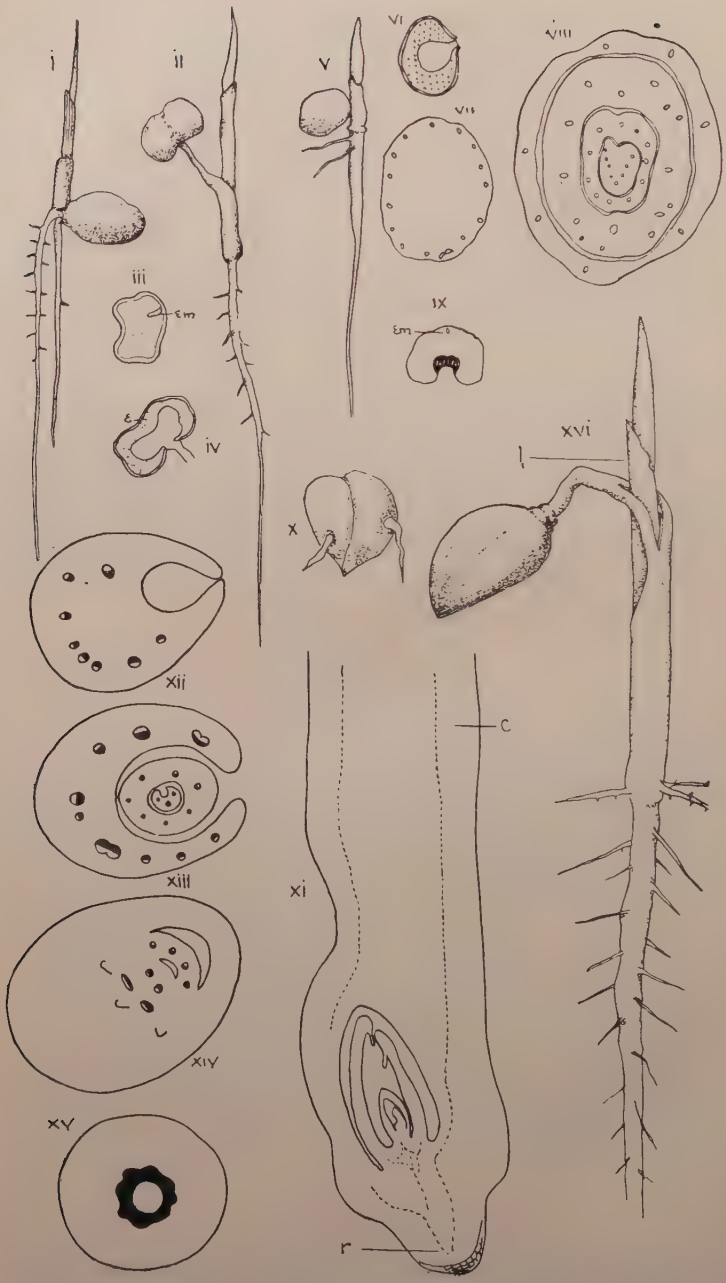

Fig. 63.

Six strands proceed from the tip of the cotyledon, four of which enter the ligule. Of the two strong and equally developed roots it was impossible to determine which was the primary root. Both produced numerous short rootlets, and the stele in each case was sclerotic. One root was pentarch, the other hexarch.

Literature on the Seedlings of Palms.

Klebs (87) places the Palms in Type 1, an inadequate treatment since every type of germination is represented in the family. Schlickum (127) described the seedling anatomy of *Washingtonia robusta*, finding six strands in the cotyledon stalk and five in the sheath, while the ligule was supplied by two strands ascending to the tip and descending. A third strand died out at the apex of the ligule. Drabble (41) disagreed with van Tieghem (146) and with Sargant (120) on their observations on the transition of *Phoenix dactylifera*. He noted that in Palms the plumular strands are later in differentiation and lignification than the cotyledon bundles, yet certain xylem and phloem strands of the root are directly and primarily continuous with those of the plumule and have a lateral connection or none with strands common to root and cotyledon. The root stele of *Phoenix dactylifera* and of *Livistona* he found to have twelve poles. The cotyledon of the former may have six or seven strands and *Livistona* fifty in the suctorial tip, but only nine in the sheath. *Oreodoxa*, *Pritchardia*, and *Coleospadix* have essentially the same

FIG. 63.—Seeds and seedlings of Palmae. i. *Areca sapida* ($\times \frac{2}{3}$). ii–iv. *Chamaerops excelsa*. ii. Seedling ($\times \frac{2}{3}$). iii. Median transverse section of seed, showing embryo in longitudinal section (actual size). iv. Spoon-shaped suctorial tip of cotyledon embedded in endosperm (actual size). v–viii. *Chamaedorea Sartorii*. v. Seedling ($\times \frac{2}{3}$). vi. Transverse section of seed and suctorial tip of cotyledon lying in endosperm (actual size). vii. Transverse section of suctorial tip of cotyledon ($\times 10$). viii. Transverse section (above the cotyledon stalk) of the ligule and young leaves ($\times 10$). ix. *Trachycarpus excelsus*: longitudinal section of ripe seed, the embryo appearing in transverse section ($\times \frac{1}{2}$). x–xv. *Cocos capitata*. x. Fruit showing the germination of two seeds (actual size). xi. Longitudinal section of a seedling figured in x ($\times 17$). xii–xv. Transverse sections of the second seedling figured in x from a level above the plumular bud to the primary root ($\times 20$). xvi. Seedling of *Latania Commersonii*: after freeing itself from the cotyledon sheath the first leaf has pierced the cotyledon stalk ($\times \frac{2}{3}$).

c = cotyledon ; *e* = endosperm ; *em* = embryo ; l_1 = first leaf ; *r* = primary root.

anatomy. The suctorial tip of *Livistona* has little xylem, a statement recalling the work of Dixon and Ball on *Lodoicea sechellarum* (40), in the sucker of which the proportion of phloem to xylem was in the ratio 8 : 1. The seed of this species weighs from twenty to twenty-five pounds, and connection is maintained between seed and plant for five years by a cotyledon stalk which lies parallel to the surface and is frequently four to five yards long (142).

Sargant (120) considered the seedling structure to have been profoundly modified by the arborescent habit since the well-developed primary root is persistent, and, in seedlings of certain genera, the first cauline root, the direct prolongation of plumular traces, surpasses it in length and thickness. She describes the transition for species of *Thrinax*, *Desmoncus*, *Areca*, and *Acanthophoenix* as well as the classic *Phoenix dactylifera*, finding large numbers for root poles and cotyledon strands. Some importance is attached to the two-fold symmetry of specified seedlings and to the bifid apex of the sucker of *Chamaerops humilis* and *C. Fortunei* (= *Trachycarpus Fortunei*). The validity of these features as evidence of the double-bundle theory was questioned by Gatin (52), whose research dealt mainly with the embryo and morphology of germination. The emphasis placed by Sargant and Drabble on transition phenomenon is lacking in Gatin's publication, which should be consulted for information regarding previous research on Palm seedlings (1588–1908).

Gatin found the morphology of germination to be connected with the embryonic structure, and described the increase in volume of original embryo cells and the cell divisions which must take place in restricted portions of the cotyledon in order that the seedling take its characteristic form. According to Gatin, the germination of Palms exhibits two phases. The first, in which the embryo elongates and emerges without cell division, ought to be considered not as the first stage of germination but as the completion of the maturation of the embryo. The second phase, in which plumule and primary root, ligule if any, and axis take up their permanent orientation in relation to one another, corresponds to the germination of the Grasses. Gatin believes the Palms to furnish evidence in favour of de Jussieu's theory (85) that the cotyledon is the first leaf of the plant.

Arborescent Type, markedly Xerophytic.

AMARYLLIDACEAE.

Vellozia elegans.

The plant belongs to a genus with stems generally thick and woody, surrounded by many fibrous sheaths. Its habit is so distinctive that, while Bentham and Hooker place it among the Amaryllidaceae, Engler makes a family for it and the genus *Barbacenia*. The tribe or family consists of markedly xerophytic plants inhabiting the dry campos of Brazil, or south and tropical Africa and Madagascar. The plants are perennial and live in " stony, sunny places with but little earth for the penetration of roots " (151). The stems branch dichotomously, and are covered by a thick coating of roots, which proceed within the leaf sheaths towards the ground. Few anatomical details are available. The leaf of *V. compacta* is composed of thin-walled transparent tissue " similar to that of the leaf of Gramineae, Juncaceae, Cyperaceae," while the adventitious roots arising within the leaf sheaths have a " thin-walled, often starch-bearing endodermis, the central part being occupied by a heavy layer of exceedingly thick-walled stereome " : an exodermis is present. Warming (151), who notes that the tree fern *Dicksonia* has a similar trunk and the same internal structure, believes that the fibrous sheath covering the trunk has the same function in each. Schultze (131) adds little to Warming's findings. Nothing whatever of the germination or seedling is recorded.

The flattened, cylindrical seed (1·5 mm. in length) has a dark brown testa. The embryo is cylindrical and straight (fig. 64). At germination a considerable quantity of endosperm remains. The cotyledon consists of a sheath less than 1 mm. long, terminating in a minute, blunt sucker. Elongation of the cotyledon sheath and hypocotyl carries the light seed above ground, and within a few days the first leaf appears. The primary root is long, tapering, and persistent. Its upper limit is marked by a ring of long root hairs. Cauline roots, often with lateral branches, are produced in the first month. The seedling has a very delicate appearance. When three weeks old its total length is less than 5 mm. The first leaf is narrow and linear in shape.

Anatomy of Seedling Three Weeks Old.—A single collateral strand (fig. 64), with xylem and phloem more or less equally developed, proceeds from the tip of the cotyledon to the base

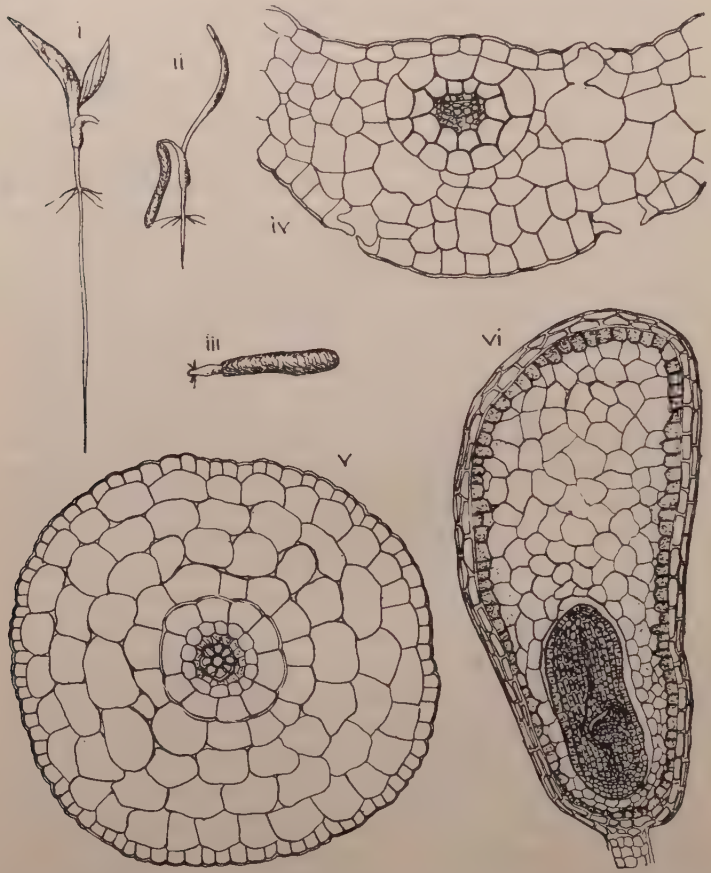

Fig. 64.—*Vellozia elegans*. i. Seedling twelve weeks old (×6). ii. Seedling three weeks old (×6). iii. Seedling two days old (×10). iv. Transverse section of the cotyledon lamina in the neighbourhood of the vascular strand (×150). v. Transverse section of the primary root (×220). vi. Longitudinal section of seed, showing ripe embryo (×40).

of the sheath, the tissues of which show some degree of differentiation. The vascular strand, which acts as a midrib, is ensheathed by eight or nine large parenchyma cells with intercellular spaces. The adaxial epidermis consists of

small regular cells, and, where aerenchyma occurs, may comprise the entire adaxial tissue. The abaxial tissue consists of spongy mesophyll, a sub-epidermal layer, and epidermis, which is interrupted by numerous sunk stomata with large air cavities beneath them. At early stages the first leaf has a mid-rib and a pair of lateral strands which, with the contribution from the second leaf, enter the hypocotyl as a single wedge. The cotyledon strand passes through the hypocotyl independent of the plumular traces which constitute the more massive bundle. The diameter of the primary root is small. The vascular structure is protostelic (fig. 64). A central xylem core, composed of a single vessel surrounded by seven others, lies within a ring of phloem. Two sheaths delimit the stele. The inner, like a pericycle, abuts on the phloem and is composed of cells thickened on all but the outer tangential wall. If the inner be regarded as a pericycle, then the outer sheath, consisting of large cells very regularly arranged, is the endodermis. The roots of the adult have a thin-walled endodermis ; while the outer sheath of the primary root does not show the thickened walls of the inner, its cells have slightly thicker walls than those of the cortex. There is no exodermis in the primary root at the stage examined.

The extreme reduction of vascular tissue in *Vellozia* finds its only parallel amongst seedlings of epiphytic and helobic forms. Its similarity to Bromeliaceae is not confined to seedling structure. The resemblance in habit and habitat was seen by Gaudichaud (59), who compared the aerial roots of *Tillandsia* and *Vellozia*, and Didrichsen (1876) examined the course of the roots in the stem cortex of *Vellozia* and different Bromeliads. Warming (151) considers the function of these roots to be the absorption of atmospheric moisture (recalling, it may be suggested, the roots of epiphytes), and the fibrous sheath of roots and leaf-sheaths is a protection against excessive drought. Similarity in habit and the problems of water supply have apparently produced a similar response in the adult. Two views regarding the seedling anatomy are possible. The protostelic condition of the primary root of *Vellozia* and the morphological resemblances of the adult plant and the tree ferns suggest primitiveness. The similarity in anatomical detail between the seedlings of *Vellozia*, the Bromeliaceae, and hydrophytic types is so striking that it is

fairly reasonable alternatively to regard it as a response to environmental conditions.

Arborescent Types showing Succulence.

Liliaceae.

Aloe.

The seed is endospermic ; it is irregular in shape, usually three- or four-sided, and is 4–7 mm. long. The embryo is cylindrical and straight.

Seedlings of nine species were examined. Germination is Type B (fig. 65). Development is at first moderately rapid. At germination little or no endosperm remains, but the seed adheres to the cotyledon tip until it rots. The sheath is the principal part of the cotyledon. In five species, namely *A. plicatilis*, *striata*, *variegata*, *Davyana*, and an unnamed species (K. 97), the sheath joins the suctorial tip abruptly ; in *A. arborea* there is a short connecting stalk ; while in *A. parvispina* the stalk is 1·5 mm. in length. Except in *A. Davyana*, there is a very short, non-vascular upper sheath.

In a week-old seedling the first leaf is 3–6 mm. long and is the dominant organ. It resembles the adult leaf in shape and in such features as the occurrence of marginal teeth, silica granules, and raphides. Succeeding leaves develop slowly. Internodes are suppressed. The plumular bud is extremely well protected in a hollow at the base of the youngest leaf, so that it is nowhere exposed. The youngest leaf is in the same manner completely ensheathed by the next oldest leaf. The cotyledon, first leaves, and to a certain extent the primary root are succulent. The primary root is persistent. Cauline roots arise when the second and third leaves appear.

Anatomy.—The cotyledon consists chiefly of water-storing parenchyma. Two cotyledonary strands follow a parallel course from the tip to the base ; the suctorial tip may have a double bundle instead of two single strands (*A. parvispina*). In order to accommodate the lengthening first leaf, the cells towards the apex of the sheath become attenuated, forming a short upper sheath.

In the species examined the primary root varies in thickness. Although the stele of *A. Davyana* is the weakest, a water-

storing cortex gives the root the greatest diameter. It may be tetrarch, as in *A. parvispina*, *Davyana*, *plicatilis*, *striata*, K. 97; or diarch, as in *A. arborea*. (The primary root of

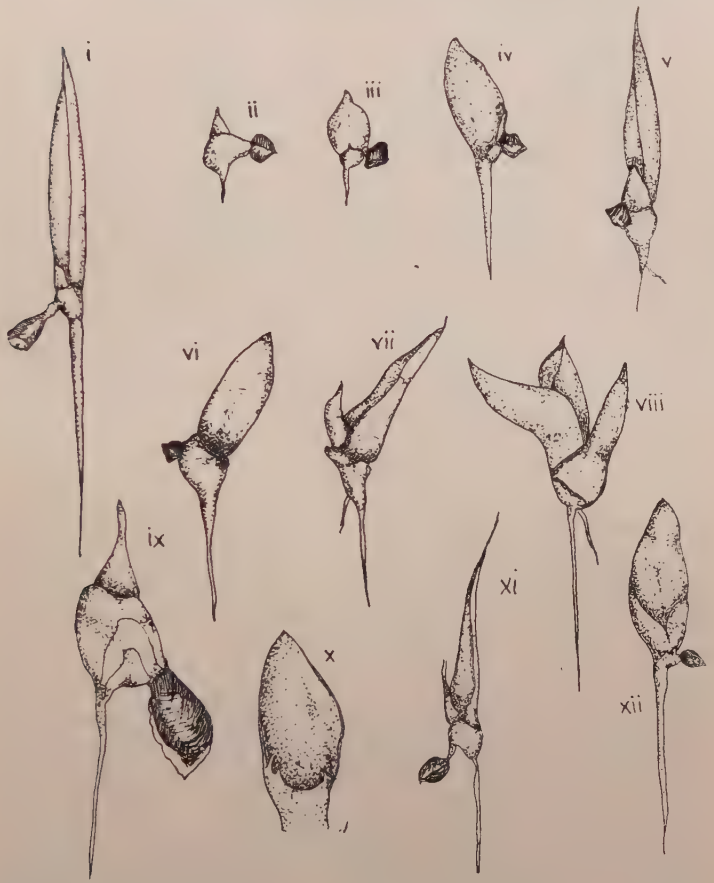

Fig. 65.—Seedlings of *Aloe*. i. *A. plicatilis* (actual size). ii–iv. Three stages in development of *A. striata* (actual size). v. *Aloe* sp. vi–viii. Seedlings of *A. Davyana* ($\times \frac{3}{2}$). ix. *Aloe* sp. K. 97 ($\times 6$); the course of the cotyledon traces is indicated. x. First leaf of *A. Davyana* ($\times 3$). xi. *A. parvispina* ($\times 2$). xii. *A. arborea* ($\times 2$).

one seedling of *A. striata* was pentarch.) *A. variegata* has a hexarch root. A suberised exodermis, having thickened outer walls, may occur below the piliferous layer. Certain of its cells are thin-walled. This feature is found in *A. variegata*, *parvispina*, *striata*, *Davyana*, and *plicatilis*. The tangential

and radial walls of the endodermis of the latter are heavily suberised. The root stele is medullated except in *A. parvispina*, *striata*, and *variegata*. (Engler notes this for the adult plant.) The cauline roots of *A. parvispina* and *A. striata* are hexarch, with a medulla.

The first leaf has three to five strands peripherally arranged. (Six occurred in *A. plicatilis* which, compared with equally old seedlings of other species, had the longest leaf.)

The only references in literature to the seedling appear to be Sargant's (120) note on six species, and sketches of a few early stages in Engler's Pflantzenreich. Sargant refers the short transition to Type III, and notes that, since the cotyledon traces are inserted on those of the plumule before or at the transition, the root depends solely on the three or four plumular traces for its symmetry. She classes *Aloe* with the arborescent type; little affinity with seedings of the latter is revealed in the present investigation.

Gasteria verrucosa.

Although all species of *Gasteria* do not produce a woody stem, the seedling is described with *Aloe*, which it resembles in external and internal morphology, rate of growth, succulence, and persistence of the radicle. The organs have a relative differentiation and development comparable to those of *Aloe*.

Anatomy (fig. 66).—The two strands of the cotyledon follow parallel courses from the suctorial tip to the apex of the sheath. A distinct stalk region is absent. The strands then diverge a little, the upper continuing horizontally before assuming a vertical direction downwards. At the base of the sheath they both join the plumular traces, which are derived chiefly from the mid-rib of first leaf. A triangular plate results. 50–60 μ lower it re-arranges itself into a diarch root stele. The first leaf is so succulent that it is almost cylindrical at the sheathing base, which, as in *Aloe*, affords protection to the plumular bud. Its vascular supply, a mid-rib and two lateral strands, is poorly developed.

Amaryllidaceae—*Agave heteracantha.*

Germination (Type A) and development of the seedling (fig. 66, viii–x) were followed until the production of the

second foliage leaf. The cylindrical, succulent cotyledon increases for some weeks in length and girth, being 30 mm. long and 4 mm. in diameter when four weeks old. The strong primary root persists and elongates at the same rate as the cotyledon. A cauline root is produced in alignment with the plumular bud. The first leaf had a toothed margin.

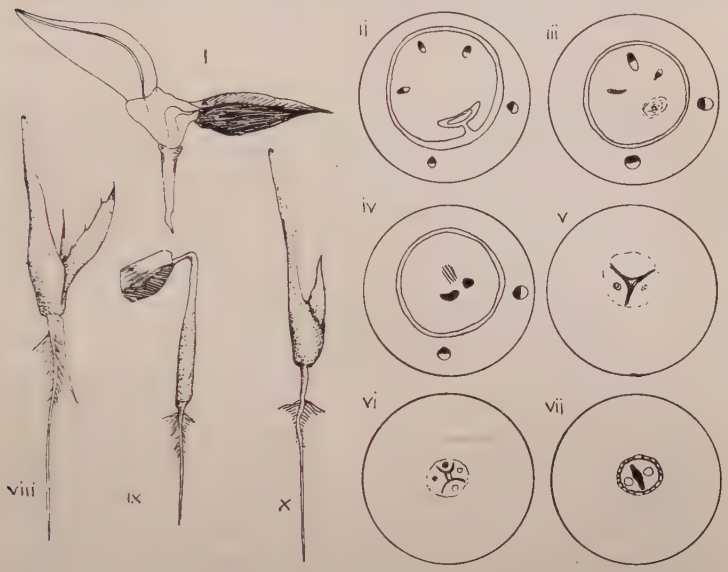

FIG. 66.—i. Seedling of *Gasteria verrucosa*; the two cotyledon strands are discernible in the succulent tissue (× 5). ii–vii. Transverse sections of seedling figured in i from the level of the plumular bud (ii) to the primary root (vii). viii–x. Seedlings of *Agave heteracantha* (× $\frac{2}{3}$).

Contrary to Lubbock's observations (97) for *A. Wislizeni*, there was a marked development of the hypocotyl (4 mm. long in oldest seedling).

Anatomy.—Throughout most of the length of the cotyledon two main and two weaker subsidiary strands are equidistantly placed. Towards the tip these converge in pairs. At the basal end the diameter of the cotyledon increases and the strands ramify, giving four main and three subsidiary strands. The ground tissue is water-storing, and the papillose epidermal cells are cutinised on the outer wall. The hypocotylar stele consists of four phloem groups placed outside a ring of xylem. The primary root is tetrarch.

Sargant (120) has described the transition for *A. spicata* and *A. Rovelliana* (= *A. Roezelliana* ?), which are characterised by the same cotyledon and root anatomy. Three or four traces from plumule and cotyledon traverse the comparatively long hypocotyl, which has stem structure. *Agave*, according to Sargant, " is designed on a Liliaceous model." In its vascular anatomy it resembles the majority of the Amaryllidaceae examined in the present study.

Summary.

The robust habit of Palm seedlings is shared by *Yucca* and *Dracaena*, but not by seedlings of other species examined. The size of the seedling has apparently a direct relation to the size of the seed, but no quantitative comparison was made of the size of the different embryos at maturity or between the size of the seedling and the quantity of available endosperm. Absorption of endosperm is rapid in the Liliaceae, slow in *Vellozia*, and exceedingly slow in Palms. The seed in Palms may be attached to the cotyledon for months and even years.

The type of germination is variable in the group, and in Palmae even within a genus (for example, *Cocos*). Epigeal germination is exceptional. Ligulate and non-ligulate cotyledons occur almost equally. The cotyledon of the non-ligulate type may have a tubular sheath merging into a short or fairly long stalk and distal suctorial tip. Where a short upper sheath, non-vascular and open, is found (as in *Aloe*), the cotyledon stalk is short. The cotyledon tip is cylindrical, save in the Palms, in which it may be spherical, concave, or ovoid. The bifid shape in certain species is doubtless related to the need for a greater surface ; that it has any phylogenetic significance is highly improbable.

The variability in cotyledon anatomy may be referred to differences in the size of both seed and adult plant. The Liliaceae may have the double-bundle system (Aloineae, *Cordyline*, and *Astelia*), or numerous strands (*Yucca* and *Dracaena*). Anatomically the cotyledon of *Agave* resembles that of the small-seeded, bulbous Amaryllidaceae. In the Palms, the ramifications of the traces and the tendency for phloem to preponderate in the cotyledon tip, suggest that the number of vascular strands is related to the quantity of

endosperm which has to be translocated. The occurrence of large numbers of vascular strands in the cotyledon is not peculiar to seedlings of arborescent types.

The primary root is lengthy, very strong, and long-lived, and may early show signs of becoming sclerosed. It produces strong lateral roots, and in the first month is supplemented by one or more cauline roots. In many Palms the first cauline root is indistinguishable from the primary root and is often in direct continuation with the plumule and not with the primary root axis or cotyledon strands. Anatomically the primary root exhibits great variation. In the small Liliaceous types the stele is triarch, tetrarch, or pentarch. There may be five to fifteen poles in the root stele of the Palms. The primary root of the Aloineae is specialised in relation to xerophily.

Development of the plumule in Liliaceae is at the normal rate for the type of germination, except in seedlings of the Aloineae, the leaves of which slowly appear. The plumular development of *Vellozia* is also retarded. According to Sargant (120) it is unusually rapid in *Yucca* and *Dracaena*. The Palms show a strong development of the early leaves. While it has been suggested (120) that the habit of these plants may be connected with the rapid production of leaves, the fact that germination is usually hypogeal cannot be overlooked as a contributing factor to the importance of the plumule. Even in the young seedling it has been found that plumular traces may have no direct connection with cotyledon strands but may be directly inserted on the primary root axis. This plan is not confined to arborescents; it is exemplified by the Commelinaceae (fig. 40). The rosette habit of the young leaves of the Aloineae was (like the lengthy primary root) observed also in the succulent Bromeliaceae.

The hypocotylar structure is common to all but the Aloineae and *Cordyline Banksii*. The plumular and cotyledonary traces tend to run independently through the hypocotyl without anastomosing, an arrangement which has been explained (120) as a device to allow for the increase in the plant's girth and the number of plumular strands. It cannot be regarded as peculiar to seedlings of arborescent forms, since it is shown in a modified form by Commelinaceae. In *Cordyline Banksii* the hypocotyl has root structure.

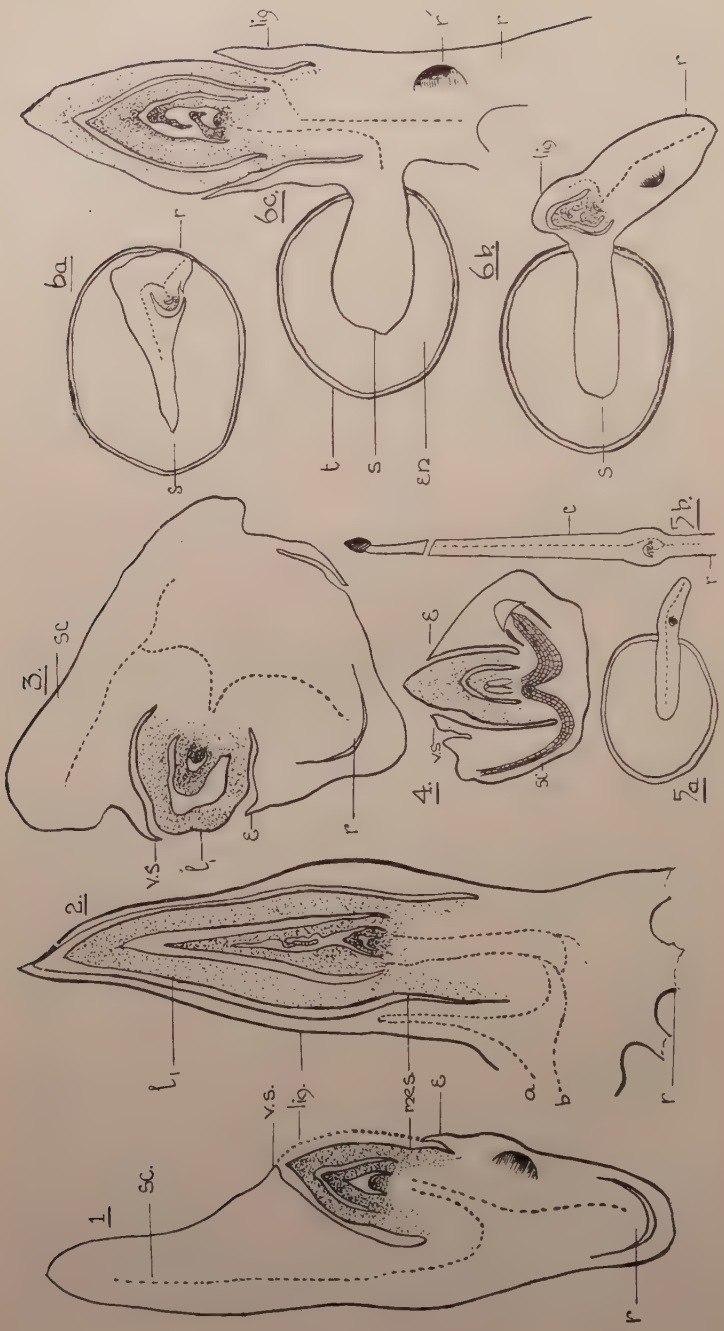
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Fig. 67.

The seedling of *Vellozia* is in a category of its own. It resembles in no respect the arborescent *Doryanthes* of the same family, described by Sargant (120). The delicacy of its appearance, its retarded development and extremely simple vascular anatomy would make it appear that features such as the structure of the hypocotyl and primary root, which might be linked with the arborescent habit, are swamped by the xerophytic character of the seedling.

The Embryo and Seedling of the Glumiflorae.

Gramineae.

The most recent reviews of the history of research on the homologies of the organs in the Grass embryo and seedling will be found in the publications of Sargant and Arber (124), Worsdell (156), and Avery (3). The present writer's views have already been elsewhere presented (16).

If the embryos of Gramineae be compared with those of other Monocotyledons, the closest resemblance will be seen to lie with embryos having an asymmetric vascular skeleton, which produce a seedling with a ligule on the cotyledon. In the Grasses the marked differentiation of the plumule, its dominance over the other organs, the endogeny and poor differentiation of the primary root, and the presence of strong initials of adventitious roots, recall the embryos characteristic of Zingiberaceae and Cannaceae. The most obvious dissimilarity is in the symmetry of the vascular skeleton, in the shape of the haustorium (which in the Gramineae is a shield-like structure, the scutellum), and in the presence in certain Grasses of a parenchymatous, non-vascular, foliaceous structure, variable in shape and size, on the axis opposite the insertion of the scutellum. In what are usually regarded as

Fig. 67.—1. Longitudinal section of *Avena sativa*: the dotted line between the ventral scale and epiblast indicates the position of tissue in a complete ligulate seedling. 2. Seedling of *Hedychium Gardnerianum* for comparison with *Avena*. 3. Ripe embryo of *Bambusa arundinacea*. 4. Embryo of *Oryza sativa* (after Bruns). *5a, b*. Germination of an epigeal type for comparison with 6. 6. *Billbergia zebrina*. *a*. Longitudinal section of seed, showing ripe embryo whose organs exhibit an orientation comparable to that of *Bambusa*. *b*. Ligule in process of formation. *c*. Seedling ten days old, showing the final orientation of sucker, shoot, and root. (Compare with embryo of *Avena sativa*.)

c = cotyledon; *e* = epiblast; *en* = endosperm; l_1 = first leaf; *lig* = ligule; *mes* = "mesocotyl"; *r* = primary root; *r'* = adventitious root; *s* = sucker; *sc* = scutellum; *t* = testa; *v.s* = ventral scale.

typical Grasses (for example, *Zea* and *Avena*) the vascular strands between root and shoot are in direct vertical continuity, while the vascular supply proceeds from the sucker at a right angle or oblique to the plumular axis. For this reason Gatin (52, 54) regarded the mature Grass embryo as showing an orientation of organs which was attained in Monocotyledons with a ligulate cotyledon only after germination at a stage which he termed "the second phase of germination." The Grass embryo has therefore anticipated in the seed a post-seminal state. Since the seedling can establish itself immediately on germination instead of having to undergo preliminary changes in orientation of the organs, a distinct advantage is gained by the whole family.

Its haustorial function has placed the scutellum indubitably as the equivalent of the suctorial portion of the cotyledon. The sucker's unusual shape, which is chiefly responsible for the peculiar superficial appearance of the embryo, is of little significance in determining the homology of the organ. Its development is slightly variable in Gramineae, and there are instances in other families of cotyledon suckers flattened like the scutellum (for example, *Musa*). The nature of the epiblast is still a matter of considerable dispute, and one of the latest papers on the subject of the Grass embryo (3) credits it with no more morphological significance than the peg of Cucurbitaceae.

On germination the root sheath ruptures the pericarp, and the primary root appears. The behaviour of the shoot region led van Tieghem (147) to classify Grass seedlings into three types : (1) the *Avena* type, in which the plumular bud and its sheath, "the coleoptile," are lifted on an elongating internode (hereafter termed the first internode), connection between coleoptile and scutellum being maintained by a peripheral vascular strand in the internode ; (2) the *Zea* type, in which elongation of the first internode was confined to its upper part, and there was no connecting cotyledon strand between the coleoptile and scutellum ; and (3) the *Triticum* type, in which the first internode remained short, the principal region of elongation being the internode above the coleoptile. The degree to which the first or second internode elongates depends on the depth of sowing (90).

The resemblance of the coleoptile to the ligule of a ligulate cotyledon and the anatomy of the first internode have been

the chief sources of difficulty in determining the homologies. Since part of the vascular structure of the first internode in certain genera was obviously derived from the scutellum, the tendency has been to regard it as a unique structure inserted between the scutellum and what was apparently the cotyledon sheath or ligule. Hence the term "mesocotyl" was commonly applied to the first internode, while the term "coleoptile" has been regarded as synonymous with cotyledon sheath. The epiblast, on this interpretation, had to be explained as an outgrowth from the scutellum, or a rudimentary second cotyledon.

Avery's recent paper (3), which came to the writer's notice after the publication of her own views, makes three important contributions to the subject. From a study of the development and anatomy of the embryo and seedling of Maize, Oats, Wheat, Barley, Rye, and Rice, Avery has shown that the differences in the anatomy of the first internode are to some extent dependent on variability in ontogenetic development, that the vascular system of the coleoptile in Grasses is no more closely connected to the scutellum than that of succeeding leaves, and that the three morphological types distinguished by van Tieghem can be reduced to one fundamental type. *Zea*, *Avena*, and *Triticum* appear different upon development because of the difference in the location of the meristematic region responsible for the initial internodal elongation. In *Avena* the meristematic zone is above the vascular plate at the scutellar node (the level at which the scutellum is inserted on the axis). The scutellar strand is carried up as a peripheral trace in the internode because the meristematic zone surrounds the scutellar bundle before elongation of the internode commences. According to Avery, the scutellar strand supplies two upward branches at the coleoptile node, then descends to the scutellum node and turns upwards again, its downward and second upward course constituting the central stele which hitherto has been assumed to consist of plumular traces. The scutellar bundle is responsible for the two bundles of the coleoptile, and for two (often four) bundles and part of the mid-rib of the succeeding leaf.

This type of anatomy is comparable to that of *Billbergia zebrina*, examined in the present study, where, in the second phase of germination, the single cotyledon strand enters the

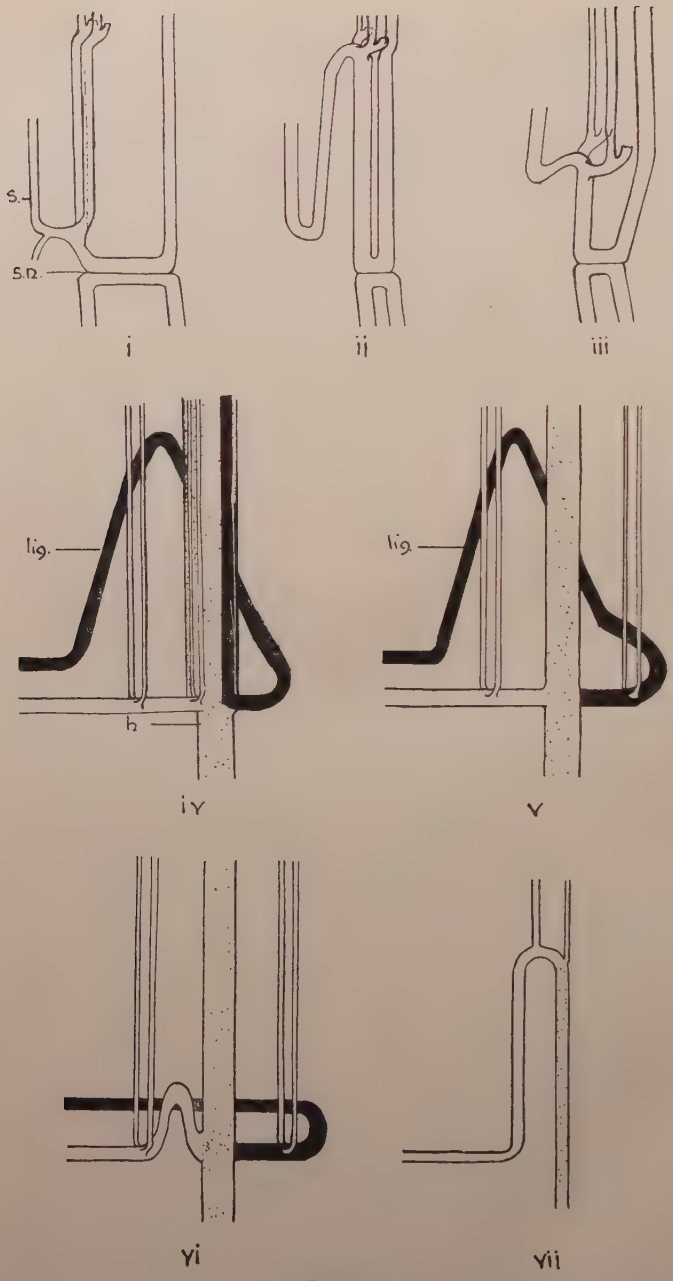

Fig. 68.

lengthy first internode of the axis and, before descending as part of the central stele, gives off branches which supply the first leaf and the meristematic tissue of the bud. Whether the strand, like that of *Avena*, turns upwards in contact with its downward course could not be definitely determined, nor was there clear evidence of a basal meristematic zone in the first internode responsible for the behaviour of the cotyledon strand. The significant point is that a normal ligulate seedling is anatomically comparable with *Avena* (fig. 67). The two seedlings are almost identical, the Grass mesocotyl and coleoptile homologising with the first internode and first leaf of *Billbergia*. The ligule of the Grass is incomplete. In *Avena* and certain genera it is partially, and in other Grasses entirely missing. The complete seedling can be reconstructed if a ligule such as that of *Billbergia*, physiologically of little significance due to the absence of vascular strands and therefore plastic, be imagined subject to reduction. That a complete ligule once existed in the Grass seedling is evidenced by its vestigial remains in such genera as *Zizania*, *Leersia*, and *Avena*. The epiblast is a fragment of its base, and the ventral scale, when it persists, represents the remnants of its apex and terminates that portion of the ligule no longer independent but fused to the scutellum. Reduction has proceeded to such varying degrees that certain genera have an epiblast extending almost to the tip of the coleoptile, while in others the epiblast is barely discernible or missing. A rough parallel between floristic advance and progressive suppression of the epiblast exists.

Fig. 68.—i. *Zea Mays*: showing strands of seedling vascular system derived at least in part from scutellum bundle. ii. *Avena sativa*, the same. iii. *Triticum vulgare*, the same. These three diagrams are after Avery (3). iv. Vascular skeleton of seedling of *Hedychium Gardnerianum* in neighbourhood of first internode; the strand shaded black passes from the cotyledon sucker into the ligule before turning into the internode. The cotyledon strand which does not enter the ligule is unshaded. The central cylinder of the first internode is stippled, but the contributions to it from both cotyledon strands are indicated. v. The same, typical of the species of *Roscoea* examined and of *Cautleya lutea*. vi. The same, *Alpinia calcarata*: one cotyledon strand bends within the internode before entering the central cylinder: the ligule is non-vascular. iv, v, and vi are, like the types of Avery, merely variations of a main type of anatomy. vii. Vascular skeleton of the first internode of *Billbergia zebrina*, whose single cotyledon strand passes directly from the sucker into the internode. (Diagrammatic.)

h = hypocotyl; *lig* = strand entering ligule; *s* = scutellum bundle; *s.n* = scutellar node.

The reduction may be traced to one or both of two possible causes. By its demands on food as well as on space the unusually strong plumule reacts adversely on the cotyledon. The ontogenetic development shows that the rim of cotyledon tissue, which in embryos outside the Glumiflorae arches over the plumular bud, leaving only a slit, is unable in most Grasses to keep pace with the differentiation and growth of the plumule; in certain ripe embryos the latter therefore projects beyond the edge of the cotyledon mass. In others (fig. 67, 3) the appearance merely suggests an unusually wide cotyledon slit. The adoption in Grasses of post-seminal orientation and differentiation in a large embryo, which, with a mass of endosperm, is confined by a firm pericarp, has evidently caused compression; the flattened sucker more than suggests a result of pressure which would also markedly affect the weak tissue at the apex of the cotyledon ligule in the neighbourhood of the slit and particularly the side in contact with the wall of the caryopsis. Of interest in connection with the effect of pressure on the embryo is the development of the viviparous *Melocanna bambusoides* (138). As the endosperm of this plant is removed by absorption, the scutellum, initially shield-like, assumes the spindle or club shape commonly found outside the Glumiflorae. The plant, which is closely related to *Bambusa*, might be expected to possess an epiblast, but the strong curvature of the embryo has caused the plumular bud and primary root to become contiguous, so that if an epiblast existed it would tend to be suppressed.

In *Triticum* only a slight elongation of the first internode occurs, since the principal region of elongation in the young axis is the second internode. When elongation in the first internode occurs, the scutellum trace is buckled up (fig. 68) and the anatomy is essentially comparable to that of *Avena* (3). The meristematic zone in *Zea* is above the level at which the scutellum trace leaves the sucker and is localised at the apex of the first internode. Avery thereby accounts for the absence of the peripheral scutellum bundle, but notes that at least part of the coleoptile vascular supply can be traced to the scutellum (fig. 68). Sargant and Arber (124) state the relationship more definitely. The anatomy of *Zea* and *Triticum*, which in Avery's opinion does not present distinct morphological types, finds a certain parallel outside Gramineae.

When in *Billbergia* and *Avena* the whole scutellum trace is carried into the first internode by the meristematic zone, short branches come from the point where the main trace is nearest the first node, and supply the first and succeeding leaves. In *Hedychium Gardnerianum* (fig. 68, iv) the first leaves are supplied by long independent branches from one cotyledon trace entering the first internode. *Alpinia calcarata* shows the intermediate condition in which a cotyledon strand gives off long branches, then ascends a short distance before bending down to join the central stele (fig. 68, vi). In *Cautleya lutea* and the species of *Roscoea* examined, the course of one cotyledon strand is considerably lengthened by being carried up in the ligular tissue before it enters the internode, after which its behaviour is identical with that of the cotyledon strand not in the ligule (fig. 68, v).

The writer's interpretation of the morphology of the grass embryo may be shortly summarised. The *scutellum* is equivalent to the suctorial tip. The *ventral scale* is the remnant of the apex of a ligule once complete; another vestige of the cotyledon is to be found in certain genera in the *epiblast*, which is a fragment of the sheathing base and part of the ligule. The origin and nature of the *mesocotyl* are purely plumular, although strands pass directly from the scutellum to the young leaves. Since the occurrence of cotyledon traces in the first internode is not confined to Gramineae, it is no longer necessary to find a theory which will allow the mesocotyl to be cotyledonary and plumular in its morphology. The mesocotyl falls into line with other first internodes, and the term "mesocotyl" becomes a misnomer. The *coleoptile* is the first foliage leaf, although it differs in shape and venation from succeeding leaves; comparable instances of a gradual transition from a scale leaf to the adult form are afforded by genera outside Gramineae (Zingiberoideae, Crocoideae and others), but the scale leaf is invariably "the first leaf." The coleoptile of Gramineae may assume the form and venation of an ordinary foliage leaf. This was recorded in the case of Elder Oats by Mr. Anderson of the Department of Agriculture Seed Testing Station, Corstorphine; and examples in other genera are cited in the literature (3). The so-called *first leaf* of Grasses is actually the second plumular leaf.

In conclusion, it is claimed that the Grass embryo and seedling are now revealed to be in much closer conformity with those of other Monocotyledons than has been hitherto supposed. Avery has convincingly demonstrated that apparent differences in the anatomy of the first internode of Grasses are not fundamental, all being variations on a single type. The writer has shown that the direct vascular connection between the first leaves and the cotyledon sucker, which *is* the fundamental feature of Grass seedling anatomy, can no longer be regarded as the monopoly of Gramineae, and has accordingly used comparative anatomy to establish the relationships between a complete ligulate seedling and the advanced Grass seedling with its reduced ligule. Her interpretation of the homologies of the " mesocotyl " and coleoptile are exactly in accordance with that of Avery, who founded his views on a study of the Grasses alone. In addition, an explanation of the significance of the ventral scale and epiblast is advanced.

Cyperaceae.

Didrichsen (1892) first indicated the unusual orientation of organs in the embryo by noting the position of the plumule and primary root. Wilczek (1892) discovered a resemblance to the Grasses in the aleurone layer which lies between the embryo and starchy endosperm. Schlickum (1896) figured a section of the embryo of *Carex folliculata*, and Goebel (61) the ripe embryo of *C. Grayana*. Kukenthal (91), in his monograph on the family, makes little reference to the embryo. The most important contribution to the subject is the recent paper of Schneider (1932), in which the development from the initial stages to the formation of the mature embryo is followed. Embryos are classified by Schneider as the *Carex*, *Scirpus*, and *Cyperus* types. *Carex* embryos, it is stated, follow the normal development ; the other types show marked peculiarities but resemble each other. The embryonic structure according to this author therefore supports Pax's division of the family into Caracoideae and Scirpoideae.

The ripe embryo of *Carex* is a pear-shaped body, the upper portion of which is the cotyledon sucker, while the primary root, protected by a root cap, is directed towards the

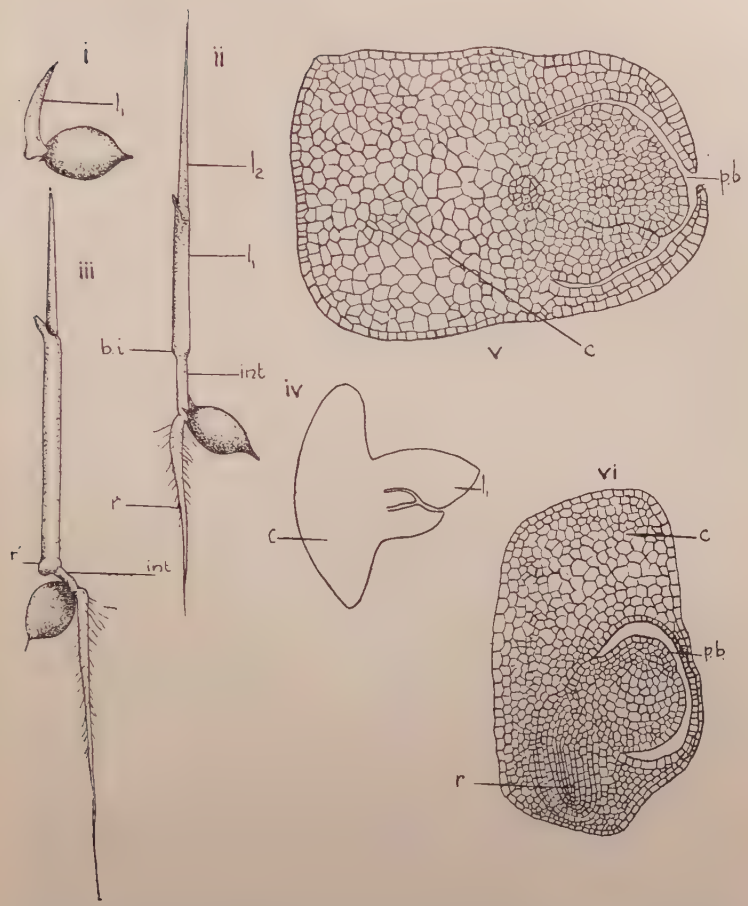

FIG. 69.—i–ii. Two stages in development of *Cyperus alternifolius* (× 15). iii. Seedling of *Scirpus setaceus* (× 15). iv. Embryo of *Scirpus littoralis* dissected out from seed and viewed lengthwise ; the first leaf is directed towards the micropyle. v. Transverse section of embryo of *Carex sylvatica* at the level of the plumular bud (× 140) ; the tissue surrounding the undifferentiated mass is plumular and, at germination, is carried up by the elongating first internode. vi. Longitudinal section of embryo of *C. sylvatica*, showing plumular bud and endogenous primary root (× 140). (Embryos sketched from preparations by W. E. Evans.)

b.i = base of first internode ; *c* = cotyledon ; *int* = first internode ; l_1, l_2 = first and second leaves ; *p.b* = plumular bud ; *r* = primary root ; *r'* = position at which adventitious root will emerge.

suspensor at the narrower, basal end (fig. 69, vi). The root primordium lies at a slight angle to the cotyledon strand, which is median. The plumular bud is a lateral undifferentiated mass, exposed by a wide " cotyledon " slit (fig. 69, v). *Cyperus* and *Scirpus* (fig. 69, iv) have strongly asymmetric embryos. The suspensor and root are lateral, the position normally filled by the primary root being taken by the plumular bud, which is directed downwards towards the micropyle and is described (125) as being surrounded by the cotyledon sheath or coleoptile. The remainder of the embryo is a more or less undifferentiated mass, the cotyledon sucker. The developmental history of the *Scirpus-Cyperus* type is given by Schneider (125) in some detail. Early cell divisions follow the *Alisma* type (65), the first indication of a procambial strand being the formation of a double layer of cells which proceeds from the upper to the lower end of the embryo. Cell division in a lateral zone leads to the gradual shifting of the suspensor from the micropyle, and a small protuberance (the initial of the stem apex) and a surrounding wall (" the cotyledon sheath ") are simultaneously formed in a lateral position. The stem-bud initial becomes spherical, but the growing-point is indistinguishable. Gradually the edges of the surrounding sheath increase in size, and close over the plumular bud, leaving such a small slit that externally nothing can be seen of the plumule. The sheath appears asymmetric at maturity owing to the more rapid growth of the upper rim. Continued development is accompanied by the swinging round of the bud and its sheath to the micropyle, so that finally the displaced root and suspensor lie at a right angle to their original direction, the vascular system being correspondingly affected. The upper cell-complex of the embryo, the cotyledon sucker, enlarges further by expansion of the cells and not by cell division. Only ripe embryos of species of *Carex* and *Scirpus* were examined in the present research ; they repeat the features described by Schneider.

While a number of authors have superficially described the germination, the morphology of the seedling has received little attention. Ebeling (42) first mentioned the germination. Klebs (87) placed it in a category of its own. In 1891 Tschirch (149), in figuring the seedling of *Carex maxima*, labelled the sheath of the plumule cotyledonary, and classified the sucker

with the Palm type, since, after germination, it enlarges and bores deeply into the endosperm. Schlickum (1896) investigated the anatomy of *Carex folliculata*. He noted that the plumular bud and its sheath might be lifted on a cylindrical internode, which he termed the hypocotyl and recognised as the homologue of the mesocotyl of Gramineae. van Tieghem (147) also compared the seedling of Gramineae and Cyperaceae. In his monograph Kukenthal's (91) sole comment on the seedling, "Das Hypokotyl bildet ein kräftig entwickeltes Saugorgan dessen Oberfläche aber nicht von einem absorbierenden Gewebe überzogen wird," is in most respects inadequate. Holm (1897), who described the germination, was puzzled by the homology of the parts in seedlings developing a "mesocotyl." ". . . It seems a most difficult task to define them correctly so as to bring them in strict conformity with the corresponding organs in other monocotyledonous plants and avoid bringing their anatomical structure in contest with their rank in a morphological respect." He found a source of difficulty in the lack of an epiblast in the Cyperaceae, and suggested that in this family the cotyledon was limited to the sucker in the seed. Rendle (110) referred to the germination as differing from that of Gramineae and resembling that of Palmaceae and Liliaceae. Goebel (61) figured the seedling of *Carex*, *Cyperus alternifolius*, and *Scirpus lacustris*, noting the close parallel with seedlings of Gramineae. Schneider (125) followed the mechanism of germination, recording that in the initial stages, growth in the embryo is concentrated between the sucker and plumular bud. Elongation of the cells in this zone propels the root in *Carex* and the plumular bud in *Scirpus* and *Cyperus* out of the seed. The primary root and sheath of plumule appear simultaneously. Schneider's findings on this point disagree with those of Ebeling (42), who remarks that the sheath appears first. The primary root is initially restricted in growth ; it is assisted by a garland of strong root hairs, and later forms a root cap. Schneider confirms observations on the course of the vascular strand from the sucker into the coleoptile, but evidently did not study the structure of seedlings having a "mesocotyl."

The writer has investigated seedlings of *Scirpus setaceus*, *Cyperus natalensis*, and *C. alternifolius* (fig. 69). A simple collateral strand surrounded by a sheath proceeds from the

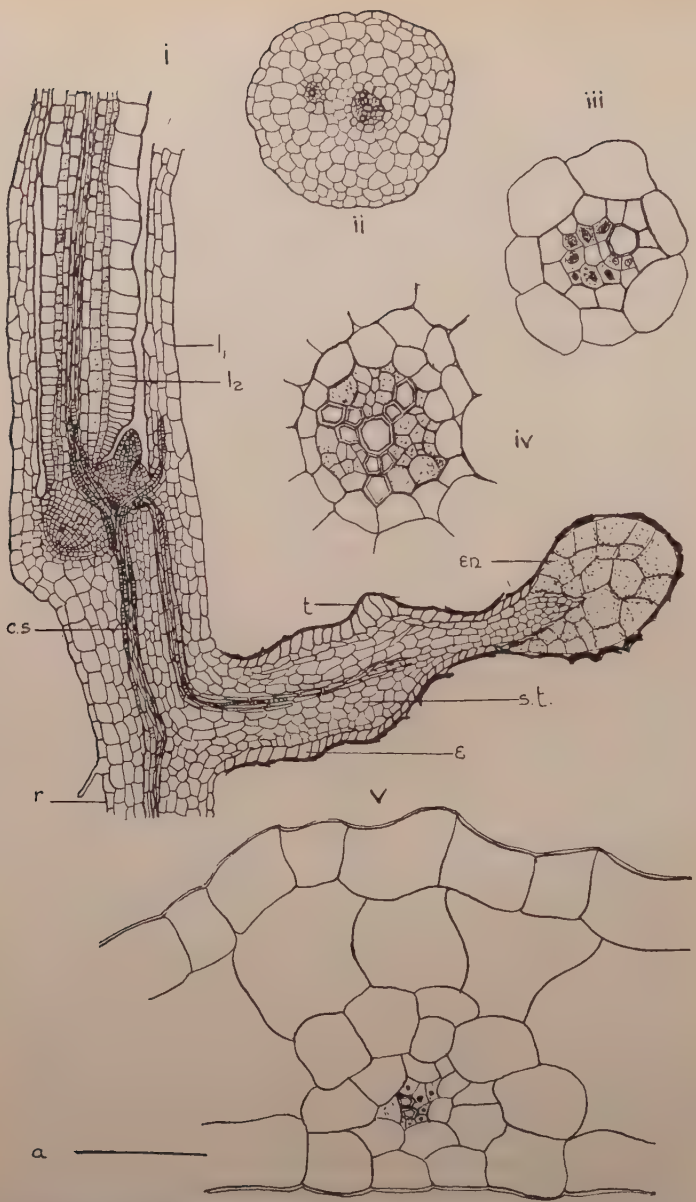

FIG. 70.—*Cyperus alternifolius*. i. Longitudinal section of young seedling; an adventitious root is seen originating at the base of the second leaf (×80). ii. Transverse section of first internode ("mesocotyl") (×75). iii. Peripheral trace (direct from sucker) figured in ii (×400). iv. Central trace (proceeding from plumular bud to root) figured in ii (×400). v. Fragment of first leaf in transverse section, showing the mid-rib which is in direct connection with the strand from the sucker (×320).

a=adaxial epidermis of leaf; *c.s*=cotyledon strand; *e*=epithelium of sucker; *en*=endosperm; l_1, l_2=first and second leaves; *r*=primary root; *s.t*=suctorial tip of cotyledon; *t*=testa of seed.

spindle-shaped sucker and ascends in a lateral position to the apex of the cylindrical stem region which has previously been interpreted as a hypocotyl, mesocotyl, or first internode of the plumular axis. The first leaf (or coleoptile), which is a sheath or scale leaf, tapering to a long green point, has only one strand, which is supplied directly from the cotyledon trace. As in Grasses, adventitious roots may arise at this node. A median strand, having usually three xylem poles (fig. 70), passes downwards from the node to the primary root.

The writer would submit that her interpretation of the organs in the grass embryo and seedling is also justifiable in the Cyperaceae. If the argument in the case of Gramineae be granted, the interpretation of the scale leaf as the first foliar organ of the plumule, and the "mesocotyl" as the lowest stem internode presents no difficulty. The green tapering tip of the sheath in certain Cyperaceae is of interest but is not regarded as evidence of its morphological rank. The cotyledon in Cyperaceae is believed to be represented solely by the sucker—equivalent to a greatly swollen suctorial tip; and the very short neck of tissue, scarcely recognisable as a distinct region, but responsible for elongation at germination of the embryo, which connects the sucker with the root and shoot, is equivalent to the cotyledon stalk in a ligulate seedling. The undifferentiation of the cell-complex is due, not to primitiveness but to rigorous reduction involving the entire loss of the cotyledon sheath even to the disappearance of the vestigial epiblast. That no embryo or seedling of Cyperaceae has yet been found to possess an epiblast or ventral scale argues a similarity to the most advanced type of Grass embryo without an epiblast, a point which Schneider, in enumerating the additional organs produced by the Grass embryo, failed to record.

The distortion of a simple embryo to the asymmetric type, the origin of the plumular bud and its sheath leaf, and even the early unequal growth of the latter, are identical in Cyperaceae and Gramineae. It is true that the Cyperaceae differ from Gramineae in having a simpler epithelium in the sucker, a larger proportion of absorbing tissue, and a primary root which is less endogenous, but these are minor differences. The only possible objection to the plumular nature of the

so-called cotyledon sheath is its origin from the lateral face of embryonic tissue which later differentiates into the cotyledon sucker. The same problem arises in interpreting the morphology of the Grass embryo. Botanists have not welcomed the idea that a sheath arising round a stem apex from a mass in which the limits of cotyledon and plumule are undefined may itself be plumular, their reluctance being traceable to a classical conception of embryological development based on primitive types (65). Simple types (fig. 72, i) have a plumular meristem which in the ripe embryo is limited in extent and appears deep-seated since its own differentiation proceeds so slowly that the neighbouring cotyledon tissue grows around it, leaving only a very small slit. The plumular bud of Gramineae and Cyperaceae appears superficial owing to its marked differentiation and rapid growth outwards from the reduced undifferentiated cotyledon mass, which cannot keep pace in development with it. Cannon (27) mentions that the plumular sheath (coleoptile) in *Avena fatua* originates *within* the low ridge of cotyledon tissue surrounding the stem tip, while Schneider describes the stem bud and sheath as being *simultaneously* produced—evidence of the homogeneity of the tissue of sheath and stem apex. As Avery (3) remarks of the Grasses, " the sheath is no more a part of the cotyledon than is the growing-point of the stem itself, but must be interpreted in the light of its later development."

The sequence in Cyperaceae in which the plumule and primary root emerge from the seed has in the past been emphasised. It is obviously related to the intra-seminal orientation of the organs. Stapf (138) found the simultaneous appearance of shoot and root in *Melocanna bambusoides*, in which the plumular bud of the asymmetric embryo is directed towards the point of its emergence. Schneider differentiates between the asymmetric *Scirpus-Cyperus* type of embryo and the more normal *Carex*, but the symmetry of the latter is secondary. The *Carex* embryo is as far removed from the normal type, since its cotyledon is also reduced to a food-absorbing spindle.

It is concluded that in seedling anatomy, early developmental history, and advanced asymmetry of the embryo, the Cyperaceae and Gramineae are closely similar, but reduction in the differentiation of the cotyledon of the former has

proceeded to a greater extent, so that all traces of an erstwhile protective function of the cotyledon have disappeared. Whether the anatomy of the first internode in Cyperaceae can, as in Grasses, be referred to a main type is a question for future research.

III. DISCUSSION.

The Morphology of Germination.

Previous Classifications.

Richard (112), in 1811, distinguished between two types of morphology of germination. In his rémotive type, elongation of the cotyledon carries the plumular bud some distance from the seed, but in the admotive type the two are in juxtaposition, since development of the cotyledon after germination does not involve an elongation carrying the bud farther from the seed. Without apparent reference to Richard's work, Martius (1823–50) applied the terms "germinatio remotiva" and "germinatio admotiva," with the same connotation, to the germination of Palms (100). An ocrea (ligule) was always present in the admotive type, which corresponds to Type C of the present work. Germination of the rémotive type fell into two categories, "germinatio remotiva tubulosa," in which only a rim of tissue round the cotyledon slit protects the young bud, and "germinatio remotiva ocreata," in which the bud is surrounded by an ascending sheath. The tubular and ocreate types are both found in the writer's Type B. Being concerned with Palms, Martius naturally did not distinguish between hypogeal and epigeal germination. The classification was excellent for describing germination in Palms, but for general purposes it is too empirical. If the terms rémotive and admotive are to be interpreted literally, the classification is faulty, for the depth of sowing has been shown (p. 105) to affect the development of the "stalk" portion of the cotyledon, hence seedlings with a ligulate cotyledon, of which the germination normally is admotive, may show a lengthy connection between the cotyledon sucker and ligule.

Klebs (1881) believed that a study of the seedling ought to take into account the time, duration, and course of germination, geographical distribution, and the natural affinities of the different genera. A complete study of germination, involving morphology and physiology, and the response of

the young plant to environmental conditions would in his opinion explain diversities unaccountable by a purely physiological interpretation. From his own research, and data from the literature, Klebs classified germination under seven headings :—

Type I. Primary root emerges first and exhibits strong growth. One end of the cotyledon remains in the seed, the other forms a short sheath.

Type II. As in Type I, but the cotyledon sheath lengthens considerably, and a filiform stalk connects seed and sheath.

Type III. Germination of the Gramineae.

Type IV. Cotyledon sheath first produced. Radicle grows in length later. This is the *Cyperus-Carex* type.

Type V. Primary root grows actively. The cotyledon becomes aerial and is the first foliage leaf.

Type VI. A ring of root hairs is produced at the upper limit of the root, which at first is undeveloped. Cotyledon as in Type V ; typical of aquatics.

Type VII. Germination of the Orchidaceae.

The work of Klebs was valuable as a record of a large number of germinations and is still quoted as a reference when a short description is necessary. It was the first classification in which reference was made to habitat as a factor influencing germination, but, in addition to its disregard of anatomy, it suffered from certain obvious defects. The length of the cotyledon stalk, which has been shown to be subject to conditions of germination (pp. 104, 105), was given a diagnostic value. Palms placed in Type I show all phases of cotyledon development. No attempt was made to distinguish between seedlings having ligulate and non-ligulate cotyledons, since both types appear in one group and ligulate cotyledons are figured in seedlings of Type I as well as Type IV. The *Cyperus* type, which shows affinities with Types III and VI, is, like the Gramineae, allotted a section of its own. Velenovsky (150) was content to refer to Klebs' classification and was accordingly criticised by Gatin (54), whose careful work on the morphology of embryo and seedling had made obvious the discrepancies of Klebs' scheme. Gatin adopted the terminology of Martius. Chouard (31) differentiates between

the form of cotyledon in hypogeal and epigeal germination, emphasising that for purposes of classification these are separate types, which he subdivides according to the proportion of sheath and stalk. He comments on the variation in type within one tribe, although Gatin (52) had noted twenty years previously in Palms the differences in cotyledon morphology within a genus.

The distinction made for descriptive purposes in the present study between seedlings with a ligulate and with a non-ligulate cotyledon corresponds in some degree to the type of germination. Ligulate cotyledons invariably are associated with hypogeal germination, while the non-ligulate cotyledon may be hypogeal or epigeal. Apparent differences in germination are directly connected with the morphology of the cotyledon and are mainly superficial. Classifications which unduly emphasise the differences not only lead to confusion but obscure the nature of the organ principally involved.

The Morphology of the Cotyledon.

The shape of the cotyledon tip, which may vary in the individual as development proceeds, is probably dependent on the nature and quantity of the endosperm and on the size and configuration of the seed, but systematic research on the question was not undertaken. The vascular supply of the cotyledon sucker is related to the physiological demands of the entire seedling. The common peripheral arrangement of the traces is related to their function. When the tip is supplied with more than three or four strands they usually ramify with no apparent system, but the number of strands counted in transverse section gradually diminishes towards the end near the micropyle. For these reasons, it seems inadvisable to attach phylogenetic importance to the shape or internal structure, although attempts to do so are recorded (9, 120).

The number of strands in the base of the cotyledon tends to be constant for a species, though not always for a genus. In seedlings of bulbous plants the original strands ramify as additional vascular tissue becomes necessary with extension in girth of the bulb. The vascular anatomy of the ligule is slightly variable even in a genus, but, as a rule, inappreciably

in a species. The course of the ligular strands has no phylogenetic significance (p. 183). The stalk of the cotyledon is a convenient portion for comparing the number of vascular strands of different seedlings. The length of the stalk but not its vascular anatomy is affected by the depth of sowing (p. 105) and by circumstances of germination (p. 104), and ought not to be given (as it has been) a diagnostic value in classification.

In epigeal germination the region between the base and tip of the cotyledon elongates, carrying the seed upwards on its tip. The same region elongates in the hypogeal cotyledon in such a manner that the plumular bud is forced deeper into the soil, frequently assisted by a contractile primary root. Morphologically the two types are identical. Physiologically the epigeal cotyledon has the additional function of manufacturing the food which it conducts, and of elaborating a photosynthetic region which is often for a season the only green member of the seedling, exemplified by the narrow cotyledon lamina of *Nomocharis* and *Lilium*, and by the broad blade of the cotyledon of *Costus* and *Paris*. The cylindrical epigeal cotyledon, seen for example in *Bowiea*, though offering a smaller surface than the flat cotyledon blade, is probably, like the cylindrical foliage leaf of certain xerophytes, an adaptation to dry conditions.

Excepting seedlings which early produce a tuber, plumular development is more rapid in hypogeal than in epigeal types. The present research therefore confirms the observations of Chouard (31) on the tribe Scilleae, and of Compton (34) on Leguminosae. The quantity of endosperm is also a factor regulating the rate of production of foliage ; if copious endosperm is available, the emergence of the first green leaf may, as the Aroideae show, be delayed. As their ripe embryos also indicate, cotyledons which protect the plumular bud by a low open sheath arising round the cotyledon slit approach the transition to the ligulate type, and clearly show the lateral origin of the ligule. They are also intermediate in having a stalk of considerable length, or its homologue, a photosynthetic blade, for the stalk is usually short and often suppressed, in the ligulate seedling. The ligule, which in its complete form is invariably associated with marked differentiation and unusually strong growth of the plumule, is a response to the need

for an elongating protective sheath for the first leaves, and originates from a portion of the cotyledon sheath in the neighbourhood of the plumular bud. In the tubular hypogeal seedling, a complete cylinder of cotyledon tissue grows actively to propel the cotyledon base deeper into the soil, a condition retained in the seedlings of the Commelinaceae which have only a short ligule. In the fully ligulate type, epinastic growth proceeds on the upper side of the cotyledon sheath after its emergence from the seed, and leads to the arching up of tissue to form an almost completely closed tube, the localised activity of the tissue producing the ligule being accompanied by hyponastic growth on the other side of the cotyledon.

To describe a ligulate seedling as having a stalk inserted at a certain level between the cotyledon sheathing base and ligule reveals an inadequate comprehension of the ontogeny, and implies that the level, at which the stalk is apparently attached, is movable with reference to a fixed length. The level of the stalk in not the determining feature in delimiting sheathing base and ligule. The " insertion " of the stalk is primarily unimportant and is the *result* of the ligular development, the variability of which is caused by a shifting of the balance of growth, a concentration, if the word is permissible, on the provision of an upper sheath, lateral in origin, protecting a rapidly growing plumule in its passage upwards, in preference to and at the expense of a sheathing base, which sinks it deeper. An appreciable lower sheath indicates a form that has not advanced far. In the extreme cases exemplified by Zingiberoideae and Cannaceae, differential growth of the cotyledon has produced a considerable ligule and consequent disappearance of the lower sheath. Evolution of the ligule has been accompanied by a gradual suppression of the sheathing base.

The vascular strands in a fully expanded epigeal cotyledon and in the tubular sheath of the simple hypogeal type proceed vertically downwards (fig. 71). The effect of disproportionate growth of part of the sheath results in diverting any strand in the affected region from its vertical course. Strands of a ligulate cotyledon not passing through the strongly meristematic region proceed unaffected, and strands in a cotyledon will pass through the ligule if part of their course in the embryo lies in the tissue giving rise later to the ligule. If a

strand in the embryo lies within but towards the edge of the meristematic zone its course in the ligule will be short. When no strand is found in a strongly developed ligule the total number of strands proceeding from the tip is low (usually two or one), and the ligule is non-vascular because the strand or strands normally proceed through cotyledonary tissue not

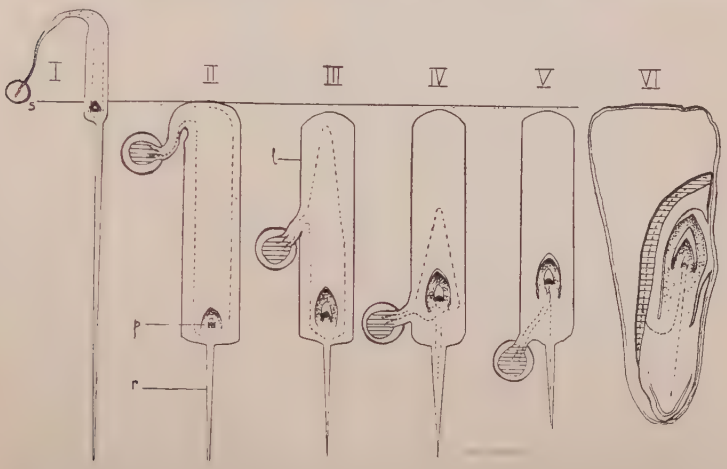

FIG. 71.—Series of Monocotyledonous seedlings, proceeding from a simple epigeal cotyledon (I) to an advanced ligulate type (V), to illustrate the gradual shortening in the course of the vascular strands of the cotyledon. The series is diagrammatic, but I–II are commonly found in Liliaceae; III represents Commelinaceae; IV–V, Zingiberaceae. The grain of *Avena* (VI) has essentially the same anatomy as Type V and an advanced differentiation and orientation of organs attained only post-seminally in other families. (The sucker is shaded horizontally, and the first internode and young leaves are stippled.)

l=ligule of cotyledon; *p*=plumular bud; *r*=primary root; *s*=surface of soil.

engaged in ligule formation. The presence or absence of a strand in the ligule must be assigned to its position in the stages before the ligule is formed. (With this in view, the variability of the ligule anatomy of *Gloriosa* is comprehensible.) Chance may have initially determined which of numerous strands would supply the ligulate tissue, but the general constancy of the ligule anatomy within a species, and to a less extent within a genus, suggests that the cells giving rise to the ligule, although indistinguishable in the embryo from tissue not involved in ligule formation, are in some way demarcated from it. The vascular tissue has been described (124) as

stiffening the ligule. The uneconomic disposition of vascular tissue which results from the pulling up of the strand in the ligule makes such stiffening a questionable advantage.

Schlickum (127) clearly recognised the ontogenetic development, " the one-sided growth of the upper part of the sheath " and its protective function, but otherwise gave it scant attention, being concerned with the ligulate type of cotyledon merely as a transition to the *Grass-Carex* type in which he supposed a " mesocotyl " (Zwischenleid) had been interposed between the ligule and stalk-sucker portion. That he was willing to argue for the origin of a simple epigeal seedling from the ligulate type weakens a masterly review on the evolutionary phases of the cotyledon. Stages before and during the formation of the ligule were apparently passed over by Sargant and Arber (124), who propounded an ingenious theory, evidently suggested, first, by the necessity of finding a fusion theory to explain the presence of cotyledon and plumular strands within the so-called mesocotyl, and, secondly, by observations on seedlings such as *Commelina*, in which the stalk makes an angle with the apex of the sheath so acute that the stalk and sheath are in close contact throughout part of their length. The single strand of *Tigridia Pavonia* ascends through a short stalk into the ligule and retraces its course from the tip to the base of the ligule, parallel to and for some length in contact with its upward course. It was suggested that the upward course of the strand in the ligule was equivalent to its passage through a stalk with which the ligule has fused throughout almost its entire length ; the downward trace represents its original passage in the sheath. But a ligule is not formed by an act such as fusion in a sharply bent cotyledon. It arises not in an angle made between sheath and stalk, but from tissue remote from the stalk at a stage when the latter, not yet defined as a narrowed part of the cotyledon, is indistinguishable from the sheath, and when the axis of the young seedling lies, at the most, in a very gentle curve (fig. 7, vii ; 67, 6*b*). Cotyledons with non-vascular ligules (Type B seedling) show no appreciable angle between stalk and sheath. Unless it is assumed that fusion between the stalk and sheath took place to varying degrees and at varying times, it is difficult to account by this theory for the widespread occurrence of the ligulate type. The

ligule appears a more normal phenomenon when regarded as merely the result of a distribution of growth whereby the sheathing base loses its identity owing to the inordinate development of part of its tissue.

The ligule has a physiological as well as a morphological significance. In the non-ligulate seedling the length of the vascular strands from the cotyledon tip through the stalk and sheath may be considerable (fig. 71, i, ii). All markedly ligulate types have been able to effect economy by abbreviating the stalk tissue. In addition, the seedlings of Zingiberaceae, of *Billbergia zebrina*, and the Grasses, which have little or no vascular tissue in the ligule, have a more direct, economical connection between endosperm, plumule, and root stele. The adoption of the ligule has allowed progress towards a more efficient and economical vascular system. Its late ontogenetic development in all ligulate seedlings, and its appearance in a degenerate form in the intra-seminal stages of the admittedly advanced embryo of Gramineae, are arguments in favour of the ligulate cotyledon as the most recently evolved type.

Factors Influencing the Morphology of the Embryo.

I. Factors concerned with its Immediate Environment.

The size of the mature embryo depends on the presence or absence of endosperm; its configuration is determined by the quantity and nature of the endosperm together with the shape of the embryo sac.

The embryonic body may be straight, or curved to a varying extent. Where curvature occurs, it is most marked in the upper part of the cotyledon, as embryos of *Alisma*, *Billbergia*, *Dioscorea*, and *Cordyline* exemplify. The remainder of the embryo and the course of the vascular meristem are apparently little affected by such curvature. How far Sargant's supposition is true (122), that its method of freeing itself from the seed influences the form of the embryo, is a question for further investigation, but it would appear that the orientation of the organs in the embryo determines the mechanism of germination and the sequence in which they appear, and not *vice versa* (exemplified by Cyperaceae, *Melocanna bambusoides*).

II. Factors concerned with Post-seminal Life.

The extent, if any, to which the embryo is influenced by the habit of the adult has been discussed in the past. From a study of Cactaceae, Ganong (51) concluded that characters adaptively acquired by the adult tend to work back into the embryo. A. W. Hill's work on *Peperomia* (68) led him to a similar opinion.

Sargant (122) believed that the future form of the seedling, itself influenced by the environment, could modify the embryo although not acting upon it directly ; slow maturation of the embryo was, for example, correlated with a geophilous habit. " Strict economy prevails during the first season of growth of the aerial parts, and the plant produces albuminous seeds with small undifferentiated embryos " (122). Evidence bearing on this question was found in the present research in the undifferentiated embryos of the Pitcairnieae and Tillandsieae, among bulbous plants, particularly in the xerophytic *Bowiea*, in the tuberous *Trillium* and *Paris*, in *Asparagus*, and in certain of the Aroideae. Yet Gatin (53) records instances of abnormal retardation in embryonic development in *Heliconia*, a tropical genus of the Scitamineae, a family in which the embryos are advanced both in structure and ontogeny.

Embryos of tuberous plants do not show tuberisation. Food storage in the hypocotyl of embryos does not foreshadow tuberisation in the young plant and adult, but is a condition found in exalbuminous seeds, correlated with the nourishment of the very young seedling. Since it occurs in embryos of aquatic and helobic species it is possibly connected with a water environment. The reserve food may be contained in the whole of the cotyledon (*Aponogeton abyssinicus*) or in a hypocotyl abnormally long (*Alisma Plantago*) or unusually thick (*Zannichellia* and *Zostera*). The aerenchymatous nature of the cotyledon tissue in the embryo of certain aquatics may be correlated with the post-seminal habit, or have an immediate value in keeping the density low to allow flotation of the seed.

The habit of the adult plant in its effect on the relative development of the primary root, plumule, and axis is traceable in the embryo to the extent to which it is reflected in the

seedling structure, the relative development of cotyledon and plumule in the seedling being, as a rule, discernible in the ripe embryo. The bulk of the embryo of *Dyckia* and *Puya*, for example, consists of the cotyledon, which is to be the first photosynthetic organ, but in the embryo of *Billbergia* the plumular bud, later the most conspicuous organ of the seedling, dominates the cotyledon. Gatin (52, 53, 54) has shown a clear connection in the Palmae, Cannaceae, and Musaceae, between the morphology of the embryo and the type of germination. The present research confirms his findings, and extends them to other families. Gatin's designations " straight " and " curved " for the embryo are not adopted in the present work, since in Gatin's sense they refer to the vascular anatomy, whereas they are commonly used of the external shape of the entire embryonic body. The curved embryo of *Alisma* is not in Gatin's sense curved. His classification of embryos (with which the writer is in entire agreement), and the relation which they bear to the germination, may be briefly summarised :—

(i) When the vascular system of the embryo can be represented by a straight line (" embryon droit ")—that is, when the cotyledonary and primary root axis are in alignment and the plumular axis parallel to them—germination is " rémotive " (p. 178) and the cotyledon of the simple, tubular, non-ligulate type. Epigeal germination is included in this category although Gatin does not refer particularly to it. The embryo and germination of *Bowiea* and *Cordyline* are typical (see also fig. 72, i).

(ii) When the cotyledonary and primary root axes are in alignment, and the plumular bud is placed obliquely to them (fig. 72, ii), germination is still " rémotive," but after germination a short sheath arises from the margin of the cotyledonary slit. Germination is usually hypogeal. This type is exemplified in certain Irises, *Asparagus*, *Aloe*, and other genera of Liliaceae and Aroids.

(iii) When the axis connecting the plumule and the primary root can be represented by a curve (" embryon courbé "), and the root cylinder lies at an obtuse angle to the cotyledon axis, then germination is " admotive " (p. 178) and the cotyledon ligulate (fig. 72, iii). The post-seminal orientation by which the plumular and primary root axes become in line

with each other but lie at an angle to the cotyledon sucker is found before germination in Gramineae.

The curvature of the axis was recorded for the embryo of *Areca Catechu* L. by Osenbrüg (104) without further discussion. Schneider's study of the embryo of Cyperaceae (125) reveals that the original procambial strand is straight, but that curvature occurs with the initiation of the plumular bud. Although

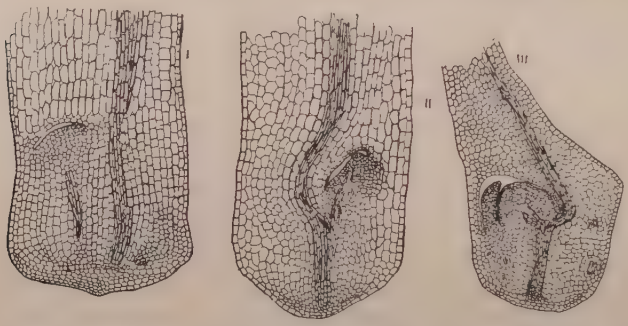

FIG. 72.—i. Part of embryo of *Dracaena Draco* (×18). This type of embryo is associated with the simplest type of germination, Type A or Type B, in which there is no attempt at an upper cotyledon sheath. Two cotyledon strands are seen in this section. The plumular traces are negligible. ii. Part of embryo of *Camassia esculenta* (×40) representing an intermediate type in which the plumular bud and its vascular traces are oblique to the main embryonic axis without markedly affecting the symmetry. Germination Type A or Type B; a low, non-vascular sheath may be produced after germination round the cotyledon slit. iii. Part of embryo of *Billbergia zebrina* (×40) representing the most advanced type with an asymmetric vascular skeleton and highly differentiated plumular bud. Germination is Type C. (Sketched from preparations by W. E. Evans.)

Gatin correlated the production of the ligulate cotyledon with the embryo having an asymmetric vascular skeleton, he failed to note that each is independent of the other, but is itself the result of unusually strong plumular development. Distortion from the simplest type of embryo (seen, for example, in *Bowiea*) originates from the vigorous development in the embryo of the plumular axis, which thrusts the cotyledon axis, the " backbone " of a relatively undifferentiated embryo, into a weaker position, being unhindered in the process by the primary root which is usually weak in the asymmetric type of embryo. The distortion after germination in the external morphology of the cotyledon can be traced to the same cause.

The degree of endogeny of the root in the embryo indicates its comparative importance in the seedling. Marked endogeny occurs in the asymmetric embryo and is accompanied by the early differentiation of cauline roots. The embryo of *Costus* is advanced with regard to its extremely strong plumular axis and cauline root system. Its epigeal cotyledon does not belong to the normal ligulate type, but the remarkable differentiation of the blade within the embryo (fig. 57) illustrates the tendency in the highest type to anticipate post-seminal changes within the seed.

It may be concluded that the morphology of the ripe embryo shows such a close correlation with the seedling structure that factors concerned with post-seminal life must be regarded as the major influence in determining its configuration; the Monocotyledonous embryo appears to be less plastic in response to its immediate environment than previous opinions would suggest.

Factors Influencing Seedling Structure.

The Size of Seed and Seedling.

The Palms, *Dracaena*, *Gloriosa*, *Hemerocallis*, *Brunsvigia*, *Crinum*, several species of *Iris*, and many others indicate that large seeds of the Monocotyledons produce large seedlings, but such a generalisation has a limited value, for no quantitative comparison of the seeds or their embryos was made.

Tansley and Thomas (140) noted the same relationship in Dicotyledons, and Compton (34) found that given uniform conditions in the seed with respect to presence or absence of endosperm and perisperm it was true of Leguminosae.

It is impossible to decide to what extent originally the type of germination (hypogeal or epigeal) was determined by the weight of the seed. Hypogeal germination occurs in almost all large-seeded types, but a definite relationship between size of seed and type of germination does not hold. Germination in the Zingiberoideae is invariably hypogeal, but *Costus* with a seed comparable in weight to seeds of Zingiberoideae has an epigeal cotyledon, while the cotyledon of many light-seeded types, such as Cyperaceae, is hypogeal. There is no exact connection between the size of seed and seedling and the production of a ligulate cotyledon. The large seedlings

of Palmae have ligulate and non-ligulate cotyledons, and all forms of germination occur among the small-seeded genera of Liliaceae. Compton (34) correlates the production of large seeds and seedlings in Leguminosae with the tree habit, but, in Monocotyledons, large seeds and seedlings characterise numerous herbaceous forms (genera of the Liliiflorae, Cannaceae, Zingiberaceae, Gramineae), while some of the smallest seeds produce arborescent types (*Cordyline*, *Vellozia*).

In the opinion of Hill and de Fraine (73) the size of seedling is a factor influencing its own internal structure since it limits the scope for evolving new types, and possibilities in large seedlings are greater since the physiological demands are heavier. It is interesting to consider how far the extension of this opinion to Monocotyledons would be justifiable. While it is generally true that small-seeded types are characterised by simplicity of structure and low numbers in the vascular system, numerous strands are associated with the cotyledon of the large-seeded Amaryllidaceae, Cannaceae, and arborescents. But the number of cotyledonary strands in other large-seeded forms (Gramineae, Zingiberaceae, Iridaceae) may be reduced to two or one, the heavy physiological demands of a well-differentiated, rapidly developing plumule being met, not by a system of numerous strands, but by economic distribution of few ; the lack of vascular tissue may also be made good by the efficiency of the sucker (well developed in such seedlings), which permits rapid translocation. An advanced embryonic structure is common to the small-seeded Cyperaceae and the comparatively large-seeded Gramineae. If it is held that the complex embryo and the seedling of the Grasses have been assisted in evolution by the large size of the organs, it must be admitted that lack of size has not retarded the Cyperaceae. In general, observations in the present research accord with those of Lee on Compositae (94), in which " there are many exceptions to the rule that the size of the seedling is correlated with the type of structure."

Possible Factors Influencing the Seedling Phase.

Before discussing the relationship of seedling structure to phyletic problems and finally attempting to analyse the factors which supposedly influence the seedling structure, a summary

will be made of evidence revealed by the external and internal morphology of the seedling.

The Cotyledon.

Epigeal germination is characteristic of all hydrophytes (except the helobic forms of the Glumiflorae), of the epiphytic Tillandsieae and Pitcairnieae, of light-seeded bulbous plants, of at least two genera of Costoideae (*Tapeinochilos* and *Costus*), of *Cordyline*, and, among rhizomatous plants, of *Trillium*, *Paris*, Rendle's "species of *Iris*" (110), *Sisyrinchium*, and *Anigozanthos*. It is successful in aquatics possibly because the danger of desiccation of the young organs is at a minimum, and abbreviation in the water-carrying system, which can be effected in hypogeal germination, is unnecessary. In epiphytes, the slowly developing Pitcairnieae, bulbous Liliaceae and Amaryllidaceae, *Trillium* and *Paris*, the epigeal habit is, in the writer's opinion, correlated with the xerophytic habit of the seedling, which involves slow differentiation of the plumule. *Tapeinochilos pungens* Miq. and *Costus speciosus* have, on the contrary, remarkably good plumular development. The hypogeal germination of large-seeded bulbous plants, and the majority of tuberous, arborescent, and climbing plants examined, may have been initially influenced by the weight of the seed ; it brings the advantage, where required, of good anchorage, which is secured in epigeal seedlings solely by the contractility of the primary root. The occurrence of the ligulate cotyledon, which is found only in terrestrial types, is independent of the nature of the storage organ, but in the material examined it was associated principally with seedlings of rhizomatous plants. A strong, well-differentiated plumule is typical of seedlings with a ligulate cotyledon. All genera examined of Commelinaceae, Cannaceae, and Zingiberoideae exemplify this relationship. Cotyledons of rhizomatous plants of the Liliaceae, Amaryllidaceae, and Iridaceae are either ligulate or non-ligulate, and this is related to variability among the genera of the development of the foliage in the adult.

The single, strongly sheathed vascular strand which proceeds through the aerenchymatous cotyledonary lamina of hydrophytes suggests a reduction from a more complex

structure in relation to the habitat of the seedling; or, alternatively, a simple primitive type, which was also unadaptable, and therefore has been confined to, or forced to colonise, a habitat which does not make too great demands upon the vascular system. While reduction may be primitive in some and secondary in others, the end result is a remarkable uniformity in the cotyledon anatomy of the group. The argument for reduction as a response to the environment can be legitimately used of the seedling anatomy of the epiphytic forms. The extreme xerophily of *Vellozia* or its primitiveness or both are reflected in the structure of its seedling.

Cotyledons with many strands are characteristic of the Amaryllidaceae having bulbiform seeds, Aroideae, Palmae, Cannaceae, certain arborescent Liliaceae, and genera such as *Costus* and *Hemerocallis*, all groups showing vigorous growth and as a rule producing large seeds and embryos. The majority of seedlings of rhizomatous and bulbous plants have two cotyledonary strands. Little can be argued from a number between the extremes associated with arborescent forms and the one strand of epiphytes and hydrophytes, but this intermediate vascular structure is consistent with the theory that to a large extent the habit of the adult plant initially regulated and is therefore reflected in the vascular supply of the seedling.

The Development of the Plumule.

With the appearance of the early leaves certain xerophytes assume the rosette habit, the aquatics the tufted habit of the adult plant. The hydrophytes produce their first leaves at a rate which is neither fast nor markedly slow. Arborescent types have strong but not unusually rapid development of the plumule. The rapid growth of *Gloriosa* is typical of climbers. The poor development of the plumule in seedlings of the Aloineae, Pitcairnieae, Tillandsieae, *Bowiea* and others is parallel to the tendency of the adult plant to reduce the leaf area. Retardation in plumular development in certain Aroids is probably related to absorption and conduction to the tuber of reserve food which would otherwise be available for leaf production, success in the Aroids, as in the bulbous forms and Medeoleae, being apparently ensured by the provision first of a perennating organ.

The Development of the Primary Root.

In general a direct relationship between the number of cotyledon strands and the poles in the root stele exists. Bulbous and tuberous plants have a contractile primary root which may function alone during the first year, or be supplemented by a single cauline root. The seedlings of arborescents have a long-lived tap root which produces numerous lateral rootlets. In climbers particularly, the primary root is remarkable for its length and strong stelar development. The behaviour of the early adventitious roots of *Gloriosa* finds a parallel in *Ornithogalum flavum* Forsk. described by Chouard (31). The long, tapering primary root of terrestrial xerophytes is usually covered with long root hairs, while epiphytes in marked contrast possess a very weak primary root or none. Although in their internal structure their affinities lie with the highly specialised Grass embryo and seedling, the Cyperaceae recall the germination of typical hydrophytes in the production of a garland of anchoring root hairs and retarded development of the primary root, features which have been correlated (87, 125) with the necessity for good fixation but not rapid absorption (though presumably the root hairs absorb). The simultaneous (125) emergence of the plumule and the primary root in the germination of Cyperaceae finds a parallel in the behaviour of the viviparous *Melocanna bambusoides* (138), a plant of forests within a heavy rainfall zone. In certain hydrophytic Grasses also, the sequence in which the root and shoot appear is regulated by the amount of available water (90).

Proceeding from transitional to advanced ligulate types, it is observed that the primary root is increasingly endogenous in the embryo and decreasingly developed in the seedling until in certain genera it is not produced as an independent organ, the loss being then made good by adventitious roots, the meristem for which is laid down before germination. The relationship lies, not between the development of the ligule and the endogeny of the primary root, but between the latter and the plumular development. (The precise anatomical relationship between the plumule and the adventitious roots is clearly shown by the Commelinaceae.) The limitations of the primary root have led to its gradual supersession by a

more efficient system of adventitious roots which supplant it at ever earlier stages of development. Amongst plants which were found to have ligulate cotyledons by far the greater number were rhizomatous. In such instances a parallel exists between the adventitious root system of the rhizomatous adult plant and that of its seedling.

The Development of the Hypocotyl.

When the plumule (as in bulbous plants) is pulled deeper in the soil by a contractile root, the hypocotyl is short or does not appear as a separate region. The study of the Commelinaceae, *Iris germanica*, and *Chlorophytum* confirms Evans' observations (45) that the length of the hypocotyl depends on the depth of sowing. If the plumular bud is too deep in the soil, the elongation of the hypocotyl propels it upwards. The length of the hypocotyl is, therefore, related to the immediate environmental conditions of the individual seedling. In seedlings with pronouncedly ligulate cotyledons the hypocotyl as a distinct organ is usually suppressed; observations on certain plants indicate that the lifting of the young leaves to the surface is then undertaken by the first internode. Such is the case in many Grasses. In the *Triticum* type, when the sowing is deep, the principal organ of elongation is the second internode. The growth of the hypocotyl of *Chlorophytum Sternbergianum*, *Amomum angustifolium*, *Amomum magnificum* Benth. et Hook. (the latter species figured (55) by Gatin), and *Wachendorfia thyrsiflora* indicates that the potentialities for hypocotylar extension are present in ligulate types, but owing to internodal activity are probably seldom called into play. A scattered arrangement of freely anastomosing strands is frequently found in the hypocotyl of seedlings in which it later becomes a storage organ. Tuberisation, once begun, noticeably influences hypocotylar anatomy. In the majority of arborescent plants examined, the plumular and cotyledon strands remain independent in the hypocotyl, allowing extension of the vascular system and increase in girth as the aerial parts develop. This arrangement possibly has a mechanical advantage in plants where stem structure is of primary importance. In two seedlings, *Arthropodium* and *Cordyline*, the stele of the hypocotyl had a radial endarch arrangement.

The Seedling Structure and Phyletic Relationships.

The form of the cotyledon has no taxonomic significance, the ligulate cotyledon being found in families with primitive and families with advanced floral structure, in isolated genera within a family (for example, *Billbergia*), and in some species of a genus and not in others (*Ornithogalum*, *Iris*).

No striking similarity in the external morphology of the seedling exists between any two cohorts or (except in the Heliobieae and Glumiflorae) between families within one cohort (Table III). The anatomical relationships within a cohort tend to be somewhat stronger.

The consistent occurrence of numerous cotyledon strands in Palms and Aroids indicates the vigorous adult (and seedling) habit, rather than kinship. The Cannaceae, Costoideae, and genera of Amaryllidaceae and Liliaceae show the same feature. Most families in which the cotyledon has two strands or a double bundle belong to the Liliiflorae. The anatomy of the ligulate cotyledon and the precocity of the cauline roots of Commelinaceae recall Zingiberaceae, but the occurrence of two cotyledonary strands in the Zingiberoideae and Commelinaceae need not indicate relationship with the Liliaceae or with each other. The seedling morphology of Zingiberoideae, like its floral characters, is an advance on the common non-ligulate Liliaceous type. Since the Cannaceae and Zingiberoideae are comparable in the habit and external morphology of their seedlings, the difference in their cotyledon anatomy is remarkable. Seedlings of Costoideae have developed along their own lines.

The heterogenity in habit of the Liliaceae is reflected in the variability of the seedling morphology. In this respect the family differs markedly from Leguminosae in which the morphology of the seedlings show "a singular uniformity which contrasts sharply with the multiformity of habit of the mature plant" (34).

The similarity in gross cotyledon anatomy between the Heliobieae and Bromeliaceae has almost undoubtedly no phyletic significance. It is difficult to estimate how far the strong resemblance in cotyledon anatomy of Bromeliaceae and the hydrophytic families (Eriocaulaceae, Pontederiaceae, and Philydraceae) is due to taxonomic relationship. Including

TABLE III.[1]

GENERAL SUMMARY.

	Germination.	Vascular Anatomy.			Habit of Adult Plant.
		Cotyledon.	Primary Root.	First Leaf.	
		Strands.	Poles.	Strands.	
HELOBIEAE:					
Aponogetonaceae	Type A	1	1 or 2	3	Hydrophytic and Helobic
Juncaginaceae	Type A	1	1 or 2	3	Hydrophytic and Helobic
Alismaceae	Type A	1	1 or 2	3	Hydrophytic and Helobic
Naiadaceae	Type A	1	1 or 2	3	Hydrophytic and Helobic
SPADICIFLORAE:					
Palmaceae	Types B and C	4–15	6–15	–20	Arborescent
Aroideae	Type B	5–7	3–5	3–8	Tuberous
	Type B	9	6	7	Rhizomatous (*Richardia*)
	Type B	1	2	3	Epiphytic (*Anthurium*)
FARINOSAE:					
Commelinaceae	Type C	2	3 or 4	5 7	Rhizomatous and Annual
Bromeliaceae	Types A, B, C	1	1	3	Epiphytic and Xerophytic

FARINOSAE:—*continued.*					
Philydraceae	Type A	1	1	3	Helobic
Pontederiaceae		1	..	..	
Eriocaulaceae		1	2	3	
LILIIFLORAE:					
Juncaceae	Type A	1	3	3	
Liliaceae	All types	..	..	..	See Table IV
Amaryllidaceae—					
Large-seeded	Type B	5–10	5–10	5–9	Bulbous
Small-seeded		2–4	3–4	mostly 3	
,, ,,	Type C	2	2	3–5	Rhizomatous
,, ,,	Type A	1	1	3	Xerophytic (*Vellozia*)
Haemodoraceae	Types A, B, C	1–4	2–6	3–5+	Rhizomatous
Dioscoreaceae	Type B	1	3	5	Tuberous
Iridaceae	Types A, B, C	1 or 2	2–4	2–7	Tuberous (see Table II) and Rhizomatous
SCITAMINEAE:					
Zingiberaceae—					
Zingiberoideae	Type C	2	3–4	5–7	Rhizomatous
Costoideae	Type A	5	..	7+	Rhizomatous (only one genus examined)
Cannaceae	Type C	7–9	..	11–20	Rhizomatous

[1] Families follow Rendle's arrangement of Engler's classification.

TABLE IV.[1]

LILIACEAE.

	Germination.	Vascular Anatomy.			Habit of Adult Plant.
		Cotyledon.	Primary Root.	First Leaf.	
		Strands.	Poles.	Strands.	
ASPARAGEAE:					
Asparagus	Type B	3–5	4–7	..	Climbing
LUZURIAGEAE:					
Lapageria	Type B	1+2	7–8	3–5	Climbing
HEMEROCALLEAE:					
Hemerocallis	Type B	4–7	5–7	10	
Funkia	Type B	2	2	3–5	
Kniphofia	Type C	2	5	3–5	Rhizomatous
Phormium	Type B	2	5	7	
Blandfordia	Type A	1	4	..	
ALOINEAE:					
Aloe	Type B	2	2, 4, 6	3–5	Succulent, arborescent
Gasteria	Type B	2	2	3	
DRACAENEAE:					
Cordyline	Type A	2	3	3	
Astelia	Type C	2	4	3	
Yucca	Non-ligulate cotyledon	4–10	5–7	8–9	Arborescent
Dracaena	Non-ligulate cotyledon	5–9	18	6–11	
Nolina	Non-ligulate cotyledon	3–4	..	..	

ASPHODELEAE :					
**Anemarrhena*	Non-ligulate cotyledon	2	4	..	Rhizomatous
**Asphodeline*		2–3	4–7	..	
**Eremurus*		3	5–6	..	
**Bulbine*		2	3	..	
**Chlorogalum*		2	4	..	Bulbous
**Anthericum*		2	2–4	..	Rhizomatous
Bowiea	Type A	2	3	5	Bulbous
Pasithea	Type B	2	5	6	
Arthropodium	Type A	2	3	..	Rhizomatous
Chlorophytum	Type C	2	2–3	5	
Trichopetalum	Type A	2	3	..	
ALLIEAE :					
Brodiaea	Type B	2	2	..	Cormic
**Allium*	Type A	2	2	..	Bulbous
**Bloomeria*		2	2	..	
**Milla*		2	3	..	
SCILLEAE :					
Ornithogalum	Type A	2	3, 4	3	Bulbous
Lachenalia	Type B	2	3	..	
Muscari	Type A	2 + 2, or 2 + 4	4–5	..	
**Hyacinthus*		2–4	..	..	
Scilla		2	2	..	
**Albuca*		2 + lateral strands	3–4	..	
**Galtonia*	Non-ligulate cotyledon	,,	3–5	..	
**Dipcadi*		,,	3–4	..	

A double bundle in the cotyledon is considered equivalent to two strands. Sargant's results are indicated *.

[1] Bentham & Hooker's classification.

TABLE IV—*continued.*[1]

LILIACEAE.

	Germination.	Vascular Anatomy.			Habit of Adult Plant.
		Cotyledon.	Primary Root.	First Leaf.	
		Strands.	Poles.	Strands.	
TULIPEAE :					
Erythronium	Type A	2	3	..	Bulbous
Fritillaria	Type A	2	4–6	..	Bulbous
Lilium	Type A	2	4	3	Bulbous
Nomocharis	Type A	2	2	..	Bulbous
COLCHICEAE :					
Merendera	Type C	2	3	5	Cormic
**Colchicum*	Type C	2	3	3	Cormic
UVULARIEAE :					
**Tricyrtis*	Type A	2	..	..	Rhizomatous
Gloriosa	Type C	2–4	2–4	9	Rhizomatous (climbing)
MEDEOLEAE :					
Paris	Type A	1+2	3	5	Rhizomatous
Trillium	Type A	1+2	3	5	Rhizomatous
VERATREAE :					
**Veratrum*	Non-ligulate	1	..	..	Rhizomatous
**Zygadenus*	Non-ligulate	1	2	..	Rhizomatous

A double bundle in the cotyledon is considered equivalent to two strands. Sargant's results are indicated *.

[1] Bentham & Hooker's classification.

Commelinaceae, families of the Farinosae appear to have reduced cotyledon anatomy. Iridaceae and Gramineae, members of which are not epiphytic or hydrophytic, show the same tendency.

The cohort exhibiting least variability in seedling structure is the Glumiflorae. The morphology of the embryo and seedling indicates not only uniformity to a considerable extent in habit, but parallel development in the embryo and seedling of both families. The intense specialisation shown by their embryos and seedlings, which is too marked to be merely accidental, provides further support of the now commonly accepted view that the Glumiflorae are a derivative and not a primitive group. The floral structure suggests reduction. Wettstein (152) derives the cohort from the Heliobieae through the Liliiflorae, and Lotsy (96) the two families independently from the Juncaceae. The embryo and seedling may be similarly derived from a simple Liliaceous type, but reduction in the differentiation in gross morphology and anatomy of the cotyledon has been accompanied by progression in other embryonic organs.

Their excessive specialisation compared with embryos and seedlings of other Monocotyledons may be accounted for in two ways. A correspondingly greater period for evolution to act may be postulated for the cohort, the derivation of which was possibly from the first group colonising the dry land. On the other hand, evolution of the embryo and seedling may have proceeded more rapidly in the Glumiflorae than in other groups. In xerophytes, for example, the habit imposes limitations ; the embryos mature slowly, the seedlings have a restricted leaf area, often in relation to elaboration of a food-storage organ. The Glumiflorae are not thus handicapped. Bews (10, 11) derives the grassland types chiefly from hygrophilous herbaceous forms with elongated jointed stems, frequently rooting at the nodes, often rhizomatous, and all responding to the demands for increasing aridity. Xerophily would not early retard ontogenetic development. Granted the escape from a habitat in which evolutionary development could only take place on limited lines (as the hydrophytic and helobic forms indicate), the embryo and seedling of Glumiflorae advanced in a direction that assured the success of the cohort. Occupying habitats which did not immediately demand

xerophilous adaptations, the adult plant (and the seedling) showed strong plumular growth which ultimately resulted in greater specialisation in the intra-seminal phase. The dominance of the cohort, which has not evolved towards elaboration of the flower for insect pollination, is in great measure traceable to the advanced state of development and orientation which the embryo attains in the seed, and to the efficiency of the vascular system of the seedling. The more rigorous reduction of cotyledon tissue in Cyperaceae points either to a group more ancient than the Grasses or, their origins being equally remote (and this agrees with the growing consensus of opinion), to a greater plasticity in the embryo of Cyperaceae, related possibly to longer, more uniformly hydrophytic conditions.

Regarding relationships within a family, the seedling structure is of interest. Seedlings resemble members of their own sub-family more closely than the members of a related sub-family. This is strikingly exemplified by the Costoideae, which entirely differs in seedling structure from Zingiberoideae. When the generic resemblances in a family are strong it is most difficult to differentiate between the seedlings of the species. Variability between the species is common in such features as the anatomy of the root stele and first leaf (Crocoideae), the nature of glandular hairs (Bromeliaceae), epidermal cells (Commelinaceae). The organ least affected by specific differences is the cotyledon. Its anatomy is invariable within a genus except when the habit varies or when the strands are numerous ; the cotyledon anatomy of a species may then vary, and fluctuation occur to a less extent in the root anatomy.

The main points of interest relating to seedling morphology which arise from the foregoing review will now be briefly discussed.

(*a*) The separate organs of the seedling do not show advance uniformly. The tendency in the most specialised type of seedling (of which the cotyledon is ligulate) is towards dominance of the plumule.

(*b*) Evolution has not proceeded at the same rate in its effect on the seedling and reproductive phase. Simplicity or reduction of the flower may accompany a highly evolved

seedling structure (Gramineae), and one family may show amongst its genera (obviously equally advanced floristically) all grades of evolutionary development in their seedlings (Liliaceae, Palmae).

(*c*) Certain families exhibit a remarkable uniformity in seedling structure, parallel to a uniform habit in the adult. Seedling structure does not define the genus, but the seedlings are so distinctive in appearance that the family is identifiable. Where the seedling structure of a family is widely variable, the habit of the family is heterogeneous. The characteristic seedlings of certain tribes may be then recognisable.

(*d*) A scheme for the identification of a plant by its seedling would not be parallel to that founded on floral characters; this agrees with the results of research on seedlings of Dicotyledons (34, 49, 72, 73, 93, 94, 136). Only if the classification of Monocotyledons were founded on habit would the seedling have a diagnostic value, a point of interest considering that in the early attempts at classification, habit was often a leading character.

(*e*) The occurrence in certain genera of advanced seedling morphology confirms the opinion that they belong to derivative groups. When unrelated genera have a similar, highly specialised seedling structure (*Billbergia*, *Hedychium*, *Avena*) parallel development is clearly demonstrated.

(*f*) It is to be expected that the critical seedling phase will show suitability to its own environment. Thus, in aquatic and helobic forms, the epigeal germination and provision for immediate fixation by the rapid development of a shallow root system is particularly appropriate. Early submerged leaves differ from floating leaves produced later (*Typhonodorum*, *Sagittaria*, *Alisma*). Vivipary (*Melocanna*) and the germination of certain helobic Gramineae (90) afford further examples of suitability to the environment. The habit of such seedlings has become permanent. Apart from such fixity of habit, the individual seedling may possess potentialities for responding to its immediate environment. This is exemplified by the extension of the hypocotyl and cotyledon stalk in instances of deep sowing.

(*g*) The relationship between the habit of the adult and seedling must now be more closely examined. Previous workers who have found a correlation between the habit of

the adult and seedling have commented on it in a somewhat similar fashion. Hill and de Fraine (72) describe the adult of *Persoonia lanceolata* as having to a considerable extent influenced the seedling—" the characteristic external morphology may be thrust back, as it were, into the seedlings." Ganong (51) concluded that as the form of the adult in Cactaceae " becomes more and more intensified, it tends to work back into earlier and earlier stages in the ontogeny of the successive individuals, until finally a structure adaptively acquired by the adult works back into the epicotyl, and finally into the embryo." A. W. Hill (68) states that in *Peperomia* " the initiation of the necessary structural modifications which appeared first in the adult would begin to be thrown back into the early stages of the plant's development until finally the structure of the embryo would itself become involved."

Granted similar environmental conditions for seedling and adult (which do not always occur in nature), this point of view, not necessarily the present writer's, involves three implications:

(i) *That at some earlier evolutionary stage the adult showed a greater suitability than the seedling to the environmental conditions.*—This cannot be readily visualised.

(ii) *That the seedling shows more primitive characters than the adult, but the primitive phase shortens as evolution proceeds.*—This is the logical outcome of the theory that ontogeny repeats phylogeny. What has been regarded as possible evidence of the retention of relatively primitive features during the juvenile phase is provided by various conifers in which the seedling bears youth needles (134), by the transition from a simple to a more complex leaf in the Dicotyledons (notably in Leguminosae), and in Monocotyledons by those aquatic forms which first produce linear leaves and later floating and aerial leaves of different shape. Conclusive evidence from the present investigation is lacking. The production of young leaves which are smaller than the adult type is not regarded as an indication of an ancestral feature, but finds an explanation in the physiological limitations of the seedling phase. Apart from the aquatic types, transitional forms towards the adult shape of leaf were produced only when germination was hypogeal and very obviously in the highly evolved seedlings of Zingiberoideae. The production

of early scale leaves is with equal justification referable to the immediate environment of the seedling. The scale leaf rolled into a tube has a firm tip which, like the apex of the cotyledon, is doubtless of the greatest assistance in boring a passage towards the surface. The first leaf (or coleoptile) of Grasses, the behaviour of which has been experimentally studied (90), provides a familiar example. The ontogeny of the Monocotyledonous seedlings will again be referred to.

(iii) *That the habit of the adult directly affects the seedling structure.*—This could only be demonstrated if there are features in the seedling not connected with seedling survival but directly related to the adult habit; for example, if the seedling phase is passed during a cool, wet season and the adult phase in hot, arid conditions, xerophytic adaptions in the seedling might be sought. Such extremes in the environmental conditions of seedling and adult life are not associated with the genera examined by the three authors quoted nor the types described in the present publication. As far as Monocotyledons are concerned, the direct effect of the habit of the adult on the seedling accordingly remains an open question. The perpetuation of a certain seedling structure depends on the survival value of the adult which the seedling produces. The success of a particular adult form therefore determines the type of seedling structure which will persist; only seedlings with suitable potentialities provide the adult form which is appropriate to the environment. With this meaning only can it be said that the habit of the adult *directly* affects the seedling structure.

A similar environment of seedling and adult might find a similar response in each (or even a more marked response in the seedling phase), so that the habit of the adult finds a parallel in that of the seedling, and therefore appears to have impressed itself upon the seedling. Features of survival value to the adult will also make for success of the seedling, and the adult habit will be predictable from the seedling morphology. This has been commonly found in the research. The variability according to the habit in the development and anatomy of the primary root, the retarded plumular development of xerophytes, the aerenchymatous cotyledon of hydrophytes are among the most obvious examples which are too numerous to cite.

(*h*) The habit of the seedling may produce structures of significance in germination and not directly referable to the influence of other factors. The production of a cotyledon ligule has no real phylogenetic significance ; it occurs (often in isolated genera) in all the geophytic families examined. Like the endogeny of the primary root, it is traceable to strong plumular development. The environmental conditions are to be correlated with the ligulate cotyledon only so far as they allow rapid differentiation and growth of the plumular bud.

(*i*) The number of cotyledon strands in certain genera is considerably less than for related genera having a similar external morphology in the seedling and vegetative habit in the adult. It therefore appears that factors tending to reduce the vascular tissue of the cotyledon, but having no connection with phylogeny or the habit, are at work.

The Early Ontogeny and Anatomy as Indicative of Ancestral History.

The ontogenetic development of the embryo and seedling points to the derivation of the ligulate from the simple tubular cotyledon, and to the biologic trend increasingly to equip the embryo for its post-seminal life by impressing on it seedling characteristics. Tansley and Thomas (140) consider the early ontogeny of spermatophytes to be dependent on the habit of the intra-seminal embryo, and Sargant (122, 123) held that ancestral features would tend to be better preserved in the early post-seminal stages ; Horwood (80) criticised Sargant's evidence as being based on embryological features at a stage too early for recapitulation to be observed. Such statements are seen in their application to be too generalised. The present study confirms and extends Gatin's observations (54) that there is no sharp demarcation between ontogeny before and after germination, since features peculiar to the seedling stage of certain genera may be found in the precocious embryo of others. It has also been shown (p. 186) that embryonic and seedling structure are so intimately connected that no advantage is apparently to be gained in a search for phylogenetic clues by choosing late embryonic in preference to seedling stages for study.

Paris polyphylla and *Trillium ovatum* provided the only instances in the present study of stelar ontogeny sufficiently

slow to be of interest, development being usually too rapid to provide convincing evidence of a theoretical phylogenetic sequence. Much emphasis has previously been placed (33, 73, 118, 140, 143) on the anatomy of the transition. No attempt was made to fit the transition anatomy of the seedlings into types by the present writer, who considers the matter one of little phylogenetic significance. Angiospermous seedlings are confronted with the common problem of arranging the strands between root and shoot in a manner consistent with their number, the available space, and phyllotaxy. That certain members solve the problem in an identical fashion no more implies an intimate relationship than the Dicotyledonous arrangement of strands in the hypocotyl and stem of the young Monocotyledon indicates its dicotylous ancestry (105, 122). For a similar reason, speculation on the extent to which diarchy and tetrarchy in the primary root indicate primitiveness (140, 143) has been avoided.

A comparison of the anatomy of *Anemarrhena* with Ranalean forms and the common occurrence in Liliaceae of a double bundle or two single bundles in the cotyledon (regarded as the product of fusion of two cotyledons of the Dicotyledon, each with a single bundle) provided the grounds for Sargant's theory (118–122). *Anemarrhena* was regarded as primitive and the starting-point from which have been derived most, if not all, vascular types characteristic of Liliaceous and other Monocotyledonous seedlings. The discovery of a dual vascular symmetry in the cotyledons of gymnosperms and Dicotyledons weakened the theory. Another possible objection to it was the explanation of all types as deviations from a Liliaceous model. The double bundle might, in the writer's opinion, be viewed more consistently, not as the origin of anatomical variations, but merely as a stage in a lengthy series, represented at one end by the cotyledon with many strands as in Palms and Aroids, culminating in the cotyledon having one strand (seen in genera of Gramineae and others). Reduction may, however, affect the vascular anatomy of the cotyledon (and even, as in Glumiflorae, the gross morphology) while advance and specialisation take place in other embryonic and seedling organs. One character, such as the vascular supply of the cotyledon, cannot therefore be chosen as a criterion in attempting to assess phylogenetic positions.

The First Leaf.

Its proximity to the cotyledon has made the first leaf of Monocotyledons a subject of some interest (2, 85, 87, 122, 127).

The cotyledon mid-rib and vascular strands are usually symmetrically disposed opposite the mid-rib or two main strands of the first leaf.

Where germination is epigeal, the cotyledon and first leaf have the shape and vascular symmetry of the first leaf, but the latter often has additional lateral traces (*Costus speciosus*, *Paris polyphylla*, *Trillium ovatum*, *Bowiea volubilis*, *Lilium monadelphum* and others). This observation agrees with that of Schlickum (127), who found the closest parallel between the cotyledon and first leaf in the epigeal hydrophytes and Liliaceae, and with Chouard's findings in the Scilleae (31). In hypogeal germination the resemblances are less close. Chouard compared the hypogeal cotyledon of certain genera with the scale leaf of the bulb. The ligulate cotyledon is generally associated with a first leaf of the nature of a scale, anatomically simpler than later leaves. In the Glumiflorae, the first leaf takes on the protective function of the missing ligule. The early leaves of Zingiberoideae show a transition in internal and external morphology between the first leaf, which is a sheath, and the third leaf, which has the complete adult form. Klebs noted this phenomenon in Dicotyledons. In *Costus* the differentiation in the embryo of the assimilatory tissue of the cotyledon, which has the shape and the ligule of a foliage leaf, indicates the fixity in this genus of the epigeal habit.

It is concluded that if the cotyledon was not primarily a leaf its function in certain species as a photosynthetic organ has led to its assuming the characters of the first leaf.

Evolution of the Seedling.

The present study affords no direct evidence on the origin of the seed leaf, but furnishes information on its subsequent evolution. The primitive cotyledon was probably a sucker, undifferentiated and plastic as it is in the early development of the individual. It has evolved along the lines of progressive elaboration in the epigeal type and of progressive simplification in hypogeal seedlings. The plumule of the epigeal

seedling being freed from early photosynthesis developed slowly, often while the cotyledon provided a food reserve, a type suited to geophytic, frequently xerophytic, conditions thus arising. The hypogeal cotyledon, which evolved either independently or from the epigeal type, allowed shortening of the cotyledon vascular tissue and more complete protection of the plumular bud. Its existence as a subterranean organ was made possible by a large store of endosperm, more commonly by very rapid plumular development.

The provision of a ligule allowed economy in two directions. The sheath for the plumule was not provided until it was required, and then kept pace in growth with the young internodes and leaves ; at the same time further abbreviation of the vascular system of the cotyledon occurred. The demands of the plumule therefore led to specialisation of the cotyledon tissue for its protection, and consequent distortion of the cotyledonary vascular symmetry. In certain genera, the strands were ultimately diverted to the developing bud. In the most highly evolved embryo and seedling, the inordinate plumular development has caused the reduction and suppression of the ligule (for the existence of which it was primarily responsible), since the cotyledon tissue is unable as in primitive embryos to arch over the bud, which appears superficial. The strong differentiation and growth of the plumule in this type of embryo influence the orientation of the cotyledon and root strands to such an extent that the cotyledon is forced into a lateral position. The initial handicap of the lateral origin of the plumule is overcome in the Glumiflorae by the ultimate changes in the ripe embryo, and in typically ligulate seedlings by the early changes after germination. In Cyperaceae, in which evolution has been accompanied by the most rigorous reduction, the cotyledon appears once more as an undifferentiated sucker, but the condition is secondary.

By a somewhat devious course the advanced Monocotyledonous seedling has according attained, early in the ontogeny, the advantages of a lateral haustorial organ and a terminal plumule which is in direct vascular continuity with the cauline roots. The precocity of the latter in the Monocotyledon compensates for the limitations of the vascular cylinder of the primary root.

IV. SUMMARY.

1. Types of germination, external morphology, and anatomy of Monocotyledonous seedlings from every important family except Orchidaceae are described.

2. For purposes of description three types of germination (fundamentally the same) are distinguished. A simple tubular cotyledon, hypogeal or epigeal, is regarded as more primitive than the ligulate cotyledon, the possible derivation of which is discussed.

3. Features in addition to the ligulate form of cotyledon tend to occur in the seedling with advanced morphology.

(*a*) The primary root is endogenous and is early supplemented or supplanted by an adventitious root-system.

(*b*) The vascular tissue is disposed in a manner consistent with efficiency and economy, strikingly exemplified in genera in which direct connection is made through the internode between the plumular bud and sucker.

(*c*) The well-differentiated plumule, owing to its rapid development and its distorting effect on the vascular anatomy of the cotyledon, appears pseudo-terminal in the very young seedling or even in the embryo.

4. The embryo and seedling of Glumiflorae are represented as the most highly evolved. Their morphology is interpreted by a comparison with seedlings possessing a complete ligule and an advanced anatomical structure which are outside this cohort. Plumular dominance has reacted adversely on the cotyledon, whose ligule and vascular tissue have been reduced to a minimum.

5. Homoplastic development of the cotyledon and its vascular tissue is clearly shown by seedlings of genera in Bromeliaceae, Zingiberaceae, and Gramineae.

6. Evolution in the seedling has not proceeded at the same rate as in the reproductive phase.

7. The factors which supposedly influence the seedling structure, and the extent to which the habit of the adult plant can be correlated with the morphology of the seedling, are briefly analysed.

8. In a consideration of the age and possible polyphyletic origin of Monocotyledons the revealed wealth of structural detail and the tendency for specialisation in form and function of the cotyledon are significant.

In conclusion, the writer expresses her great indebtedness to Professor Sir William Wright Smith for facilities for research in the laboratory at the Royal Botanic Garden, and to his University staff. The investigation was made possible not only by the wealth of material available from the Garden but by the assistance afforded by the staff of the Propagating Department under Mr. L. B. Stewart and Mr. R. E. Cooper.

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Notes on the Collection of British Mosses in the Herbarium at the Royal Botanic Garden. By The President.

(Read 11th February 1932.)

The collection of British Mosses in the Herbarium at the Royal Botanic Garden is a fairly large and complete one. It has been over a century in the making and many individuals have contributed. It is not only intensely interesting botanically, but is even more so for the biographical and human interest which it possesses. The names of collectors eminent in their day and still remembered as botanists; the places where they found the specimens; and even the dates of collecting have all something to tell of their enthusiasm in pursuit of their hobby, whether on a public holiday or on a private one extending to a few days or weeks.

The founder of the collection was probably Robert Kaye Greville, shortly after he came to Edinburgh in 1816. It contains many of his specimens gathered in the years 1819–21, but localities are not indicated. Between 1830 and 1840 he spent the months of the long summer vacation in his native county of Durham and gathered large numbers of mosses. He was also an artist with pen and pencil. Many of his specimens are gummed to sheets of paper and are accompanied by beautifully coloured sketches on a large scale of moss leaves and capsules. In 1855 Greville collected many specimens in Perthshire; he stayed at Bridge of Allan, and from that centre he thoroughly worked the surrounding district. The banks of the rivers Teith, Leny, and Allan, together with Ben Ledi and the mountains of Breadalbane, all helped day by day to fill his vasculum.

This Society was instituted in the year 1836. Its herbarium was united to that of the University in 1839. A perusal of the *Transactions* for the next twenty years shows that the study of Muscology was taken up by some of the Fellows with much enthusiasm. Large contributions of specimens were received from several workers in various parts of the country. A large number of Irish mosses were sent by a William

Christy. Thomas Drummond of Forfar contributed many rarities from Angus. William Gardiner and William Jackson, both of Dundee, also sent large numbers from that county. W. Gourlie, G. J. Lyon, and R. M. Stark were assiduous workers in the West of Scotland.

Richard Spruce, who became a Fellow in 1842, gifted many specimens from the counties of York and Durham. James Ward added a good few from Yorkshire. Thos. Kirk explored the counties of Gloucester, Stafford, and Warwick. Wm. Mitten, a well-known cryptogamic botanist, gifted a large number from Sussex in 1846. Ten years later Alexr. Croall of Montrose and A. O. Black of Forfar were very diligent in their native county of Angus. They crossed to Fifeshire and were associated with Charles Howie in the finding of some new Brya on Tent's Muir. *Bryum Marrattii*, *B. Warneri*, and *B. calophyllum* were then new to Britain. They were also found in the same year (1853) near Southport in Lancashire.

In the early fifties Wm. Wilson of Warrington was collecting material for his Bryologia Britannica. There are many specimens of his in the Herbarium, gathered chiefly in the Midlands and Western Counties of England, as well as from North Wales. The publication of his work in 1855 gave a great impetus to the study of mosses. Charles Howie of Largo was in constant correspondence with Wilson. His letters to Wilson are preserved along with Wilson's Herbarium in the British Museum. Howie published a Moss-flora of Fife and Kinross. He presented many of his mosses to this Herbarium, but his type collection for Fifeshire, along with a considerable number from Ross-shire, collected in the company of Charles Jenner, is in the possession of Kirkcaldy Naturalists' Society.

In the years 1866 and 1869 John Sadler, then assistant to Professor J. H. Balfour, collected large numbers of mosses in the Pentlands, and the mountains of Perth and Angus.

In the early seventies George E. Hunt of Manchester contributed many mosses from Wales, the Lake District, and many parts of the Scottish Highlands. The finest specimens in the Herbarium, both as regards quantity and quality, as well as rarity, were sent by him.

Wilson's Bryologia was followed by Berkeley in 1863,

Hobkirk in 1873, and Braithwaite, who issued the first part of his monumental work on British Mosses in 1881. These volumes in their turn served to maintain the study of this most interesting group of plants.

To the list of ardent botanists in the county of Angus was at this time added the name of another, who proved himself as a discoverer of new species to be greater than any of his predecessors. The Rev. John Ferguson of Brechin spent most of his leisure time among the mountains of Clova. He added many notable plants to the British Flora, many of which are in the Herbarium.

The largest addition made to the Herbarium at one time was when the representatives of James M'Andrew handed over his collection after his death in 1917. It consisted of about 7000 packets of mosses. He had been an assiduous collector for about forty years. For many years he was parish schoolmaster at New Galloway. Botany was his hobby, and he was a recognised authority on mosses, hepatics, and lichens. He explored the Galloway country thoroughly, adding very considerably to a knowledge of the distribution in the South of Scotland. In August 1880 he visited the Rev. Mr. Ferguson at Brechin, who gave him a large number of rare alpine mosses. The Herbarium is fortunate in having these as the collector's own herbarium was by his express wish destroyed. Later, M'Andrew made several excursions to the Perthshire hills in the company of Peter Ewing of Glasgow and gathered many fine specimens, chiefly from Ben Lawers and Ben Laoigh. On his retiral in 1901 M'Andrew removed to Edinburgh. He became an Associate of this Society. From time to time he contributed several papers to its *Transactions*. Along with Allistair Murray and William Evans he made a systematic survey of the moss-flora of the three Lothians, adding many new records to the Census Catalogue then in course of compilation by the Moss Exchange Club. It was his habit every summer to spend a few weeks at a different centre rich in cryptogamic plants. From the counties of Fife, Perth, Stirling, Argyll, and the Clyde Isles he brought many specimens of mosses, hepatics, and lichens which to-day enrich the Herbarium. Besides all this work of his own he had many correspondents with whom he exchanged specimens. Thus his collection included rarities

from the Hebrides collected by Dr. James Stirton; from Cornwall and Devon by Wm. Curnow; from Oxford by Henry Boswell; from Kent and Sussex by E. M. Holmes; from Yorkshire by Wm. West; from Derby, Lancashire, and the Lake District by the Rev. C. H. Binstead; from Northampton, Sutherland, Ross, and the Western Isles from H. N. Dixon; and also from various parts of Ireland. Recently Wm. Edgar Evans presented to the Herbarium a large number of mosses gathered by his grandfather and father in the counties of Peebles and Selkirk, the Lothians and Fifeshire. Many of them had passed through the hands of Mr. Dixon, the authority on the subject in this country. Mr. Robert H. Meldrum had also named or verified a considerable number. The late Wm. Evans's collection included quite a few species from St. Kilda and the Isle of May, which he visited on several occasions.

Col. Henry Halcro Johnston has contributed many mosses as well as flowering plants from Orkney. In addition to those above mentioned large numbers of specimens have been received from various muscologists in different parts of the country.

The institution of the Moss Exchange Club in 1896 and its expansion in 1922 into the British Bryological Society was instrumental in attracting many botanists of both sexes. Through the exchange of specimens among the members many species not found in Scotland have found their way to Edinburgh.

There are at present recorded in the British Isles 625 species of mosses. Of these, only 36 are not represented in the Herbarium. But as 17 of them have been gathered only once, chiefly on Ben Lawers, it is not surprising that the Herbarium does not possess a specimen. A few found only once in England are probably now extinct, as their boggy habitats have been altered by drainage. A few mosses not in the Herbarium have been recorded from only two localities. So it is only the rarest which are awanting. Of the many varieties of some species there is a good representation.

The 625 species are divided among 114 genera. Some genera contain only one species. The genus *Hypnum*, on the other hand, contains 55 species with many varieties. There is not a single genus unrepresented in the collection, and there

are several large genera without a single species awanting, or at most only one. There are very fine specimens of some of the rarest. Thus *Saelania caesia* and *Grimmia unicolor* from Clova ; *Blindia caespitosa*, *Eurhynchium cirrosum*, and *Bryum arcticum* from Ben Lawers ; *Leucodon albidum* from Hampshire ; *Grimmia anodon* from Arthur's Seat ; *Orthotrichum Shawii* from Ayrshire ; *Fontinalis seriata* from Hereford ; *Grimmia andraeoides* from Snowdon ; and *Cinclidotus riparius* from Worcester ; and a few others have only been found in these single localities in the British Isles. Of some value, and of great interest, are specimens of a few species which were gathered for the first time in Scotland and even in Britain.

The oldest plants in the collection are dated 1778. They were gathered by Archibald Menzies, at one time employed in the Edinburgh Botanic Garden. He became a famous botanist, and towards the end of the eighteenth century explored North-west America. His herbarium was bequeathed to the Botanical Society in 1842. Besides his own gatherings it contained many mosses sent him by Dr. Hooker in England and Dr. Taylor in Ireland.

A Census Catalogue of British Mosses based on H. N. Dixon's Handbook is published by the Bryological Society, and is now in its third edition. Mr. J. B. Duncan of Berwick-on-Tweed is the editor. A supplement will be published shortly as many new vice-county records have been made in the past six years. Nearly 400 have been found in the Herbarium here.

These notes were followed by a brief account of the life-history of mosses illustrated by lantern slides, together with a statement of the method and basis of classification.

The Scottish Alpine Botanical Club Excursion, 1931.

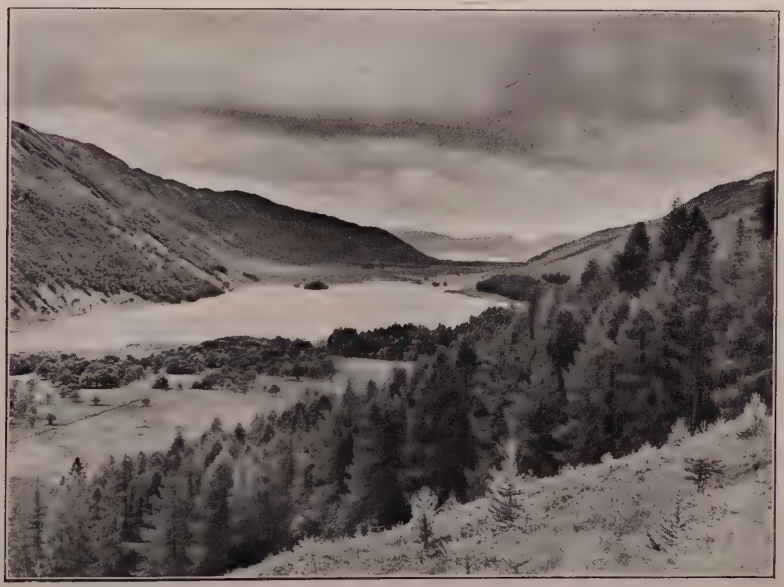
By Robert Moyes Adam, F.L.S. (With Pls. I–II.)

(Read 17th October 1932.)

17*th July*.—The Club made their base for operations at Strath Carron in West Ross. The journey was made by the West Highland route to Mallaig, thence by sea passage to Kyle of Loch Alsh, where train was taken and the run to Strath Carron completed and, despite the start at 4.30 a.m., proved so enjoyable that the party felt amply recompensed for the early morning infliction. There are few tourist journeys in Scotland that can outshine this one, and the memory remains of a continuous panorama of Highland scenery of the most fascinating type. The charm of the Mallaig section derives much from the extraordinary engineering employed in its construction.

From Fort William the railway skirts Loch Eil, the sea loch which forms the innermost reach of Loch Linnhe, where in meadows giant plants of *Platanthera bifolia* reared heads and threatened to lure the party from the train. After Loch Eil the sea is left and a pass entered down which flows the Callop River, a wild stream set among birch woods and where a few hoary Scots Pines add a sombre tone. Beyond this valley Loch Shiel and Glen Finnan come to kindle memories of the fateful days of August 1745, when the Standard was raised in favour of Prince Charlie, a scene viewed with fine effect from the wonderful curved viaduct which spans the River Finnan. Farther west the line pursues a course by the Amhainn Shlatch and ascends steeply to the watershed, and thereafter an easy gradient leads to the picturesque sheet of water called Loch Eilt, a lake of exceeding charm, studded with tree-clad islets and set amid rugged slopes whose bases are clothed by forests of oak and birch. Tree growth in this area seemed to be good and some stately conifers and thriving plantations at Glen Finnan were remarked on. At Loch Ailort contact with the sea was again made, and off and on remained in sight as headland and promontory were crossed by this highly diverting railway. A pause by the train at

An Ruadh Stac, height 2919 feet, and the barren slopes around Loch a Mhuillin, composed of Cambrian quartzite rubble, supporting scanty vegetation and occasional plants of *Arctostaphylos alpina*.



Strathcarron and entrance to Glen Carron, with Loch Dhughaill (fresh water) in the middle distance and Loch Carron (sea loch) beyond, the afforested slopes of Achnashellach in the foreground.

Robert Moyes Adam.

Arisaig provided a view of this charming village scattered around a bay with a background of woodland of subtropical luxuriance. Morar followed with a memorable glimpse of exquisite white sands.

Seawards the views were marred somewhat by low visibility, and the Isles of Rhum and Eigg, which lie a few miles to the westward, had their summits curtained in mist. At Mallaig terminus the first stage of the journey ended, and the party sought steamer for the passage to Kyle of Loch Alsh. The port of Mallaig offered little attraction to the Club who, while recognising it commercially, had its industry rather thrust upon their notice by the " Ancient and fish-like smell " that pervaded everything. It was, therefore, with a sense of relief that the party saw the gangway hauled aboard the steamer and the distance widened between them and Mallaig.

The sail to Kyle was accompanied by a delightful calm and the conditions on deck were most pleasant for observing the coastal scenery. From Mallaig the vessel crossed the seaward entrance to Loch Nevis—a fjord whose upper reaches were awesome under a leaden sky. Knoydart was skirted while its noble summit of Ladhar Bheinn was hidden by cloud. The steamer route lay inshore for a time and near enough to note the naked and barren nature of these slopes which lie exposed to the full effect of south-westerly gales. In striking contrast were the well-timbered slopes and smiling crofts of Sleat—the long arm of Skye which lay on the port side and filled the western horizon. From Knoydart the course was set for the Sound of Sleat. Loch Hourn was passed on the right, and at Kylerhea the Sound proper began. The strait is the scene of violent tides, and as the vessel proceeded enough was seen to show the dangers that beset small craft when making the passage.

Kylerhea is one of the ferries to Skye, but the steamer did not call. On the mainland opposite the remains of the Bernera Barracks, which housed the English troops in Jacobite times, were noted. As the voyage continued northward the strait widened, and before long the vessel was gliding over the calm waters of Loch Alsh. In the distance, and just discernible inshore, the grey walls of Eilean Donan Castle indicated the entrance to Loch Duich and the wild, delectable

country of Kintail. Bearing west for a few miles, the narrows of Kyleakin were approached, and shortly after the pier of Kyle of Loch Alsh hove in sight. The trouble of disembarking over, it was found that an interval of three hours must elapse before the final phase of the journey to Strath Carron could commence. The time was filled in by a stroll by Loch Alsh, where some fine plants of *Pinguicula lusitanica* and specially fine forms of *Sedum anglicum* were collected.

About 5 p.m. the party entrained for the last stage of the journey and incidentally to receive some delightful impressions of West Ross. As the train steamed along the shores of Loch Carron the seaward views of mountain and loch were unforgettable. Plockton with the promontory and islets, Duncraig with the fine plantations looked enchanting in the soft light of a summer evening. As Strome Ferry was passed the newly acquired Forestry Commission property was noted. Attadale a little later caught the President's eye, for the garden there was to be included in the Club's itinerary. Finally, Strath Carron, and at the station the eventful journey ended. Some time later an addition to the party arrived on the west-bound train, and when dinner was served a complete party assembled. After dinner the party motored to Achnashellach, where they were received by Mr. F. D. Stewart Sandeman, and in the growing dusk were piloted round his garden to see a galaxy of Chinese Primulas, among which many Forrestian species were recognised. Reluctantly, about 10.30 p.m., Achnashellach was left behind and a return made to Strath Carron.

18*th July*.—On the morrow, through the kindness of Mr. Sandeman, an automobile and chauffeur were placed at the disposal of the Club, and at 9.30 a.m. a start was made for Kinlochewe. This journey was facilitated by the private road from Achnashellach to Glen Torridon, and while on their way enabled the Club to exchange greetings with Mr. Sandeman and party who were preparing for a day's fishing on Loch Doule. The private road to Torridon ascends rapidly behind the lodge of Achnashellach until it reaches a height of 800 feet, from which point a wonderful view is obtained of Strath Carron. From the summit the road bends to the north and after a long winding descent reaches Coulin. About Achnashellach the slopes are now Forestry Commission

lands and are the scene of promising plantations. On the way to Coulin groups of native Scots Pine were noted and admired and near the Lodge form quite a forest. The scene at Coulin Lodge is one of great beauty and is enhanced by the presence of the two lochs, Coulin and Clair, which in their setting, and shores fringed with forest, form gems of their kind.

Loch Coulin held a splendid array of the white Water Lily, and reminded the Club that a former tenant of Coulin had quite a collection of exotic Water Lilies acclimatised in bog pools on the hillside nearby. Time forbade the fullest investigation of this part and the journey continued to Kinlochewe, where the car halted. In the bog below the hotel a search was made for *Eriophorum alpinum*, the plant alleged picked in August 1930 by Professor Fernald of Newfoundland. The search proved fruitless, and towards the end of the same day a further hunt was made in company of Dr. Wilmott of the British Museum and Mr. Druce of the Linnean Society. These gentlemen had details as to the site, but even with their aid no further light was shed on the " amazing discovery." The Club were interested to note the community of plants growing over the site and the principal members noted were : *Scirpus caespitosus*, *Carex pauciflora*, *Eriophorum vaginatum*. Fernald, who was unfamiliar with Scottish Botany, may have been mistaken and his " find " cannot be verified by specimens.

After the hunt for *Eriophorum* the President and another member paid a flying visit in the car to Gairloch and on the way were able to admire the beauties of Loch Maree.

Another section of the Club ascended the slopes of Beinn Eighe.

Later in the day the Club rejoined forces and proceeded, after tea at Kinlochewe, to Torridon. For mountain grandeur Glen Torridon has few rivals, and where the stupendous cliffs of Leathach are thrown down sharply to the road the scene in this glen is most impressive, an effect which was intensified by the gloom of a threatening thunderstorm. It was nearly 8 p.m. when the shores of Loch Torridon were left behind, and halting to pick up one member who had denied himself the grandeur of Glen Torridon for the glamour of the old forest at Coulin, a fast run enabled the party to reach Achnashellach in time to inspect Mr. Sandeman's catch of sea trout, and

after collecting a sample through their kindness made a quick return to their base at Strath Carron.

19*th July*.—The following morning plans were made to visit the gardens of Attadale and Courthill, and after a late breakfast the Club made their way by car to the latter. The route followed the Shieldaig road by the wild pass called the Cuag Glen. At Courthill Lady Ann Murray graciously received the party and proceeded immediately to escort them round her garden. The garden is the work of fifty years' patient industry, and bore eloquent testimony to Lady Ann's zeal and skilful cultivation. Several interesting plants of recent introduction were seen. A handsome specimen of *Meconopsis Wallichii* measured over 8 feet in height. There was both a formal arrangement and a wild garden. It had a delightful natural watercourse running through it in one part, providing perfect conditions of cool damp shade, and for the cultivation of aquatics. Some fine Struthiopteris ferns were seen, while an arresting note was struck by a blaze of scarlet imparted to a Yew hedge by a flowering Tropaeolum. Not the least interesting part of the garden was the old boundary wall which adjoins the roadway. Its plant population was an amazing array of *Erinus*, *Arabis*, *Alyssum*, *Campanula* in flower, while interspersed were hundreds of Black Spleenwort ferns. Outside the environs of the house and garden a wealth of wild flowers was observed on the meadows, these including the three fine orchids *Listera ovata*, *Platanthera bifolia*, and *Gymnadenia conopsea*. The visit proved too short for all that was to be seen, and after thanking Lady Ann for her kindness and courtesy, the party returned to the hotel and later set out on foot for Attadale. On arrival Captain and Mrs. Schroder met them, and another interesting time was begun among the plants of their garden. The Attadale garden is well sheltered and the growth of some of the rarer shrubs was astonishing. Some remarkable plants of *Lilium tigrinum* raised from bulbils were pointed out. Iris species with rhizomatous roots did badly at Attadale. But all the shrubs of New Zealand seemed in their element. Of Rhododendron quite a host of fine plants were seen, and one of the most delightful, whose foliage and character outshone many specimens grown elsewhere, was that of *R. fastigiatum*. Big plants of *R. Falconeri* and *R. Thomsoni* were also seen. A remarkable Sycamore with

Arctostaphylos alpina. Specimen growing on Cambrian quartzite rubble on the slopes of An Ruadh Stac at 2000 feet.

Pinguicula lusitanica. A group of flowering plants growing in open situation on wet peaty soil, Glen Torridon.

Robert Moyes Adam.

a girth of 36 feet was pointed out, and the party saw the birth of a new rock garden on a little cliff which has been cleared of timber and where Captain Schroder intends to get suitable sites for shade-loving species. In the course of the afternoon the Club were entertained to tea and had the pleasure of meeting Sir Thomas Miles and party, who had just arrived by yacht from North Ireland.

After bidding farewell to the Schroders and acknowledging their kindness, the homeward journey was accomplished by car provided by Captain Schroder, and after a thrilling run over what is reckoned to be the most dangerous road in Ross-shire, reached Strath Carron without mishap. After supper one member visited the moor east of the hotel, where a large colony of Common Gulls breed.

20th July.—Next morning the Club were fully equipped for a long day on the hills, and soon after breakfast a start was made for the slopes of Torr na h'Iolaire east of Tullich sheep farm. It proved to be a hill of many interesting features, and provided for less-informed members of the party an example whereon to view the geological complexity of the Torridon series of rocks. Near the base limestone appears, and in consequence a fine belt of grassland skirts the foot of the hill. Higher up acid rocks and soil leave their imprint by heath and Scirpus moor. Cambrian quartzite comes to view on the slope and ultimately on the summit region presents a wilderness of shattered fragments. The Club objective was An Ruadh Stac and was selected as typical of these West Ross Hills. The upper shoulder of this hill presented a much glaciated surface of Torridon sandstone, and fell suddenly in the west to form a series of vertical precipices almost devoid of plant life. The summit of An Ruadh Stac is crowned by pure quartzite and reaches 2919 feet. Except on the north side the cairn is surrounded by loose scree. To the north the mountain drops suddenly to a depth of 1000 feet, presenting a shattered precipice of a most unscaleable kind. The extreme porosity of the ground bars almost every form of vegetable life. The surface is like an arid desert of rubble. One plant alone was noted colonising this territory—*Armeria maritima*. Lower down, where in shallow pockets soil had collected, stunted *Loiseleuria*, *Solidago*, and *Calluna* led a precarious life. From the summit a descent was made to

Loch a Mhuilinn where some fine specimens were seen of *Arctostaphylos alpina*. The plants were growing in quartzite rubble and were a mass of vigorous shoots upon which young fruits were borne. Over this vast waste of loose rock the dominant plant was *Juniperus nana*.

Once off the quartzite the Club were intrigued by the visit paid to a gully where a scarp of limestone provided quite a rich hunting-ground after the barren wastes of the upper levels. *Draba incana*, *Sedum roseum*, and *Saxifraga hypnoides* were among the flowers seen. In the course of the day the party had divided, one of them having to catch the west-bound train while the others rejoined and assembled for dinner in the course of the evening.

21*st July*.—For the final excursion the party returned to Achnashellach where some time was spent in company with Mr. Sandeman. Many fine conifers were pointed out as well as rare shrubs, some of which could not be determined, but notes taken for future investigation. A further walk through the garden was made before the departure of another member at the station of Achnashellach. The remainder made their way up the Coulin road to the summit, then traversing the southern slope of Carn Odhar, an approach was made towards Coire Lair. On the way the weather broke down and driving rain made the going unpleasant. On entering the upper part of the Coire it was seen that difficulty would be experienced in making much of this wild coire, now hidden by dense mist and rain clouds. The programme was, therefore, altered and a descent made to the River Lair and the stalkers' path. The gorge of the stream is of remarkable depth and harbours a wealth of ferns, while along its margin several old Scots Pines grow. In places the defile resembles a canyon and seems quite inaccessible. Later in the afternoon the remnant of the Club presented themselves at Achnashellach, where after ridding themselves of their wet clothing they dined with Mr. Sandeman's party, and late the same evening made tracks for Strath Carron.

22*nd July*.—On 22nd July the meeting terminated on the arrival of the east-bound train. The journey to Edinburgh was made by rail *via* Inverness and Perth.

Some of the plants seen: *Thalictrum alpinum* Linn., *Nymphaea alba* Linn., *Corydalis claviculata* DC., *Draba incana*

Linn., *Saxifraga oppositifolia* Linn., *S. stellaris* Linn., *S. aizoides* Linn., *S. hypnoides* Linn., *Chrysosplenium oppositifolium* Linn., *Parnassa palustris* Linn., *Sedum anglicum* Huds., *Galium boreale* Linn., *Solidago cambrica* Huds., *Antennaria dioica* Gaertn., *Gnaphalium sylvaticum* Linn., *Cnicus heterophyllus* Willd., *Lobelia Dortmanna* Linn., *Vaccinium Myrtillus* Linn., *Arctostaphylos alpina* Spreng., *A. Uva-ursi* Spreng., *Azalea procumbens* Linn., *Armeria maritima* Willd., *Pinguicula lusitanica* Linn., *Empetrum nigrum* Linn., *Listera ovata* Br., *Gymnadenia conopsea* Br., *Leucorchis albida* Mey., *Platanthera bifolia* Reich. fil., *Juncus trifidus* Linn., *Sparganium angustifolium* Michx., *Scirpus caespitosus* Linn., *Schoenus nigricans* Linn., *Carex leporina* Linn., *C. pauciflora* Lightf., *Juniperus communis* Linn., *J. nana* Willd., *Pinus sylvestris* Linn. (native), *Asplenium adiantum-nigrum* Linn., *A. viride* Huds., *Scolopendrium vulgare* Symons, *Polystichum aculeatum* Roth.

On a piece of red-deer horn *Tetraplodon mnioides* B. et S. was collected.

Of special interest were plants seen at Achnashellach, and among their number the following were identified: *Acanthopanax ricinifolius* Seem. var. *Maximowiczii*, *Genista virgata* Link, and *Potentilla argyrophylla* Wall.

OBITUARY NOTICES.

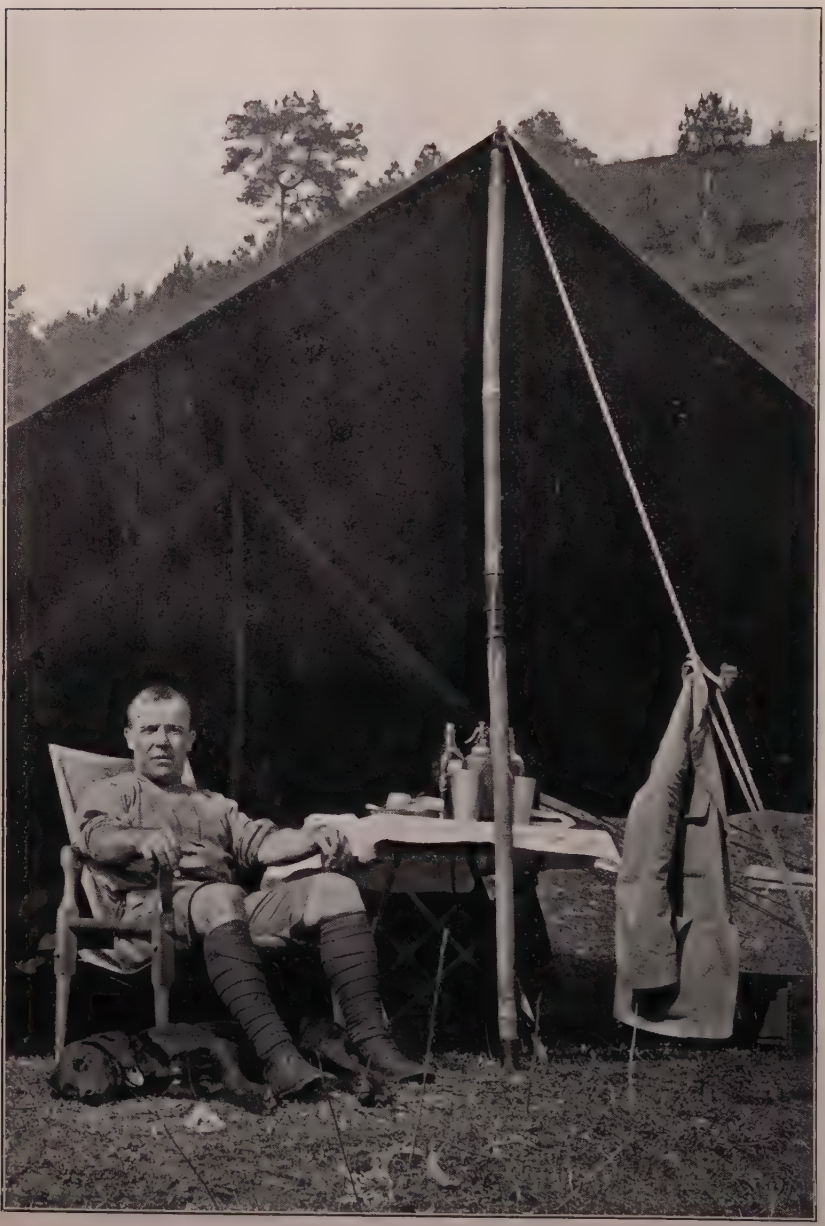
Symington Grieve.

One of our senior Fellows, Symington Grieve, died on 18th February in his 82nd year. He became a Fellow of the Botanical Society of Edinburgh in 1879, and at the time of his death held the office of Vice-President. A regular attender at the meetings of the Society and at the meetings of its Council, his keen interest and ready advice were continually asked for. On many occasions he occupied the chair, when his comments on the contribution and conduct of the discussion were illuminating. His financial aid was ever present and will be a lasting memorial of his work.

A keen observer, Symington Grieve had the advantage of much foreign travel. Notably in 1889 when he visited New Zealand, and again in 1906 when his goal was Dominica in the British West Indies. His outstanding communication to the *Transactions* of the Society was his paper on "The Floating Power of Seaweed," which aroused interest far beyond the confines of the Society.

His interests were catholic. He was a Fellow of the Royal Physical Society, to which he contributed papers on ornithology. His monograph "The Great Auk or Gare Fowl," 1885, is his most notable publication in this field. He was also a member of the Edinburgh Field Naturalist and Microscopic Society and had held office as President. Further, he was a Fellow of the Society of Antiquaries, and in 1923 published two volumes entitled "The Book of Colonsay and Oronsay."

R. J. D. G.



George Forrest.

On his 1917–19 expedition in Yunnan.

George Forrest.

1873–1932.

The Society owes a deep debt of gratitude to the late George Forrest, the eminent plant collector, a fact which was recognised by electing him an Associate of the Society in October 1927.

The following appreciation of him by Professor Sir Wm. Wright Smith is reprinted by kind permission from the Rhododendron Society Notes :—

Fate deals her mortal blow oftentimes at most inopportune and unexpected moments, and George Forrest's death on the eve of his departure for home is yet another instance of such unkind coincidence. The heavy work of the expedition was practically over and there was no mention of ill-health resulting from any of the hardships of travel. Apparently on the 6th January 1932 he had been out shooting some four miles from Tengyueh, and suddenly feeling faint he had called to his men to come to his assistance. They reached him as he collapsed, and all was over in two minutes. Men of his robust type may end thus from heart-failure. In the old sagas the heroes looked askance at a "straw-death," preferring to fall in the field. Much as we all lament his untimely passing, his end was that of a lover of the wild and of the open. He lies in the graveyard of Tengyueh, side by side with his aforetime comrade Consul Litton, who died after their adventurous journey to the upper parts of the Salwin Valley in 1906.

In this brief personal tribute to a great explorer space must be found for a glance at his early life. It is of more than passing interest to know how opportunity fashioned the man and how the man made full use of opportunity. Born at Falkirk on 13th March 1873, he had his education at Kilmarnock Academy in Ayrshire—the usual hard but withal sound training which seems to urge so many of Scotland's sons to seek their fortune abroad. On leaving school his first venture was a post in the shop of a pharmaceutical chemist. This was probably little to his liking, but he stayed long enough to acquire a useful knowledge of medicines and simple surgery, which was of great avail to him in later years when both Chinese and Tibetans sought his aid. Much of his influence with all classes in Western China was due to his generous spirit in giving both time and money to the alleviation of their sufferings. Time and again he had lymph forwarded from Burma at his own expense and inoculated thousands of the inhabitants of Western Yunnan. When he could be induced to speak of his experiences as medical attendant his anecdotes were full of self-criticism as well as of humour. As an embryo-pharmacist at Kilmarnock he had to devote some time to the study of botany and acquired an acquaintance with his native flora, collecting and drying many of the local plants. After this interlude he made his way to Australia to find what fortune he could. Here he spent several years, chiefly in the open and in the

" bush." Then was fashioned the George Forrest we knew, with sturdy frame, deep chest, and tough muscles, for he had plenty of hard work with the felling-axe, and of hard riding on the sheep-stations. There was, however, but little prospect of advancement and he returned home in 1902, making a short stay in South Africa *en route*. His previous interest in plants induced him to apply to Professor Sir Isaac Bayley Balfour in Edinburgh on the chance that employment could be found for him. Nothing was then available except a meagre post in the Herbarium, which fortunately he accepted—until something better came into view. Indoor work on dried plants was a decided change from life in the Australian bush. But as an antidote he lived six miles out of Edinburgh, tramped both ways each day to the Botanic Garden, and *stood* to his task from nine till five, disdaining the use of chair or stool. Forrest's line of choice never led him to the easy path and he was ever his own hard taskmaster. But once again chance proved a kindly guide, for his duties involved the scrutiny and arrangement of thousands of specimens from all over the world, and he acquired in these two years a sound acquaintance with the chief families and genera of flowering plants. To this experience also is no doubt due the wonderfully fine quality of his dried material—*O si sic omnes!* Any ill effects of an indoor occupation were nullified by his keenness for fishing and shooting, for tramping in hill country, and for gardening. His interest in these continued to the end. He was but little attracted by games. He may have seen in his time a football or cricket match, but in a long acquaintance I cannot recall an instance of his attendance at any sporting event where thousands congregate. The best of companions, he had no liking whatever for the town and was generally restless and unhappy there. In the country he was quite a different man. His friends will always call him to remembrance as the sturdiest of figures, clad in the trim knickerbockers which were his almost invariable wear. Determination was stamped on his somewhat grim features and he might well have borne the badge "*Nemo me impune lacessit.*" It was but rarely he offended his own feelings and those of his friends by garbing himself when occasion demanded in the clothes deemed to befit a townsman, and never was he seen in plus-fours. The ineffaceable impression he left on all who met him was that of a man who knew exactly what he wanted to do and was certainly going to do it.

To the man of thirty-one, thus fashioned and equipped, came his opportunity in 1904. Mr. A. K. Bulley of Neston, Cheshire, keenly interested in alpine plants, applied to Sir Isaac Bayley Balfour for some one who was qualified to undertake botanical exploration in Western China, and Forrest entered a field which he was never to forsake. The richness of the flora of the provinces of Western China was long unsuspected. The botanical collections of Professor Augustine Henry were evidence enough for the less westerly areas ; the material obtained by the French missionaries such as David, Soulié, and Delavay in Szechuan and Yunnan provided an abundant supply of new and interesting species for elaboration by Franchet and his co-workers in Paris ; Wilson had already begun his journeys which were to result ultimately in the publication of " Plantae Wilsonianae." But most of the evidence concerned only dried material in various herbaria and the whole of the territory was almost virgin ground for the horticultural explorer. The results of exploration work at various hands during

the last thirty years have shown that the area embracing Yunnan and Szechuan contains possibly the finest alpine flora in the world. Forrest was thus most fortunate in his lot. He began with Yunnan, and in all his eight expeditions Yunnan was ever the centre. He made incursions into alpine Burma, S.E. Tibet, and S.W. Szechuan, but he never believed even at the end that he had secured all the floral treasures of his favourite province.

On his advent in 1904 Yunnan was no peaceful country. From 1904 to 1906 he had as much in the way of perilous adventure as a man of his type could desire. The Chinese were having one of their periodical disputes with the Tibetans, and the latter did not discriminate between Chinese and other foreigners, and were massacring Chinese and French missionaries with equal zest. Forrest was at Tzekou as a guest of Père Dubernard, a veteran of the French Mission. A party of eighty (including Forrest and his seventeen collectors and servants) had hurriedly to evacuate Tzekou and flee. Overtaken by the pursuing Tibetans all were killed except a bare dozen. Père Dubernard was brutally tortured to death and a fellow-priest killed on the spot. Of Forrest's personal following only one survived. Forrest had the good fortune to escape after a pursuit of some ten days without shelter and practically without food.

To this first expedition belongs also his venturesome tour with Litton into the Upper Salwin Valley among tribes who owed allegiance neither to China nor to Tibet. Two German explorers who repeated the journey a little later were killed by the same tribesmen. The subsequent expeditions of Forrest were not fraught with the same risks as the country was relatively quiet—it was never quite free from disturbance. But Forrest's personality contributed to good relations. He was soon on friendly terms with the Chinese, with the Tibetans, and with the tribesmen of many names. He took great interest in their life and manners, doctored them by his own methods, and helped them in many ways.

One cannot venture here on any account of his various journeys, but it is needful to give a survey of the general results. His collections from Yunnan in the way of botanical specimens number over 30,000 and form the most important contribution to the flora of that province ever likely to be made. On his earlier expeditions his choice was very general, but on other occasions he devoted special attention to trees and shrubs, and especially Rhododendron, while Primula was never forgotten. Gleaners in his field will not find much in the way of flowering plants which he failed to notice, except it be in those families such as grasses and sedges where the flowers are inconspicuous or where they are natives of the warmer regions below 5000 feet. Apart from mere numbers the material is of the very highest standard and each gathering is accompanied usually by very complete notes. The copiousness and choice of the material are as remarkable as the beautiful way in which it is dried. I must here cite the opinion of a Japanese botanist, Professor Kudo, who published recently, after fifteen years' study, a monograph on the Labiatae of Eastern Asia. He visited over forty of the chief herbaria in Europe, Asia, and America, and states in his book that Forrest's specimens of Chinese plants are "die beste in der Welt."

It is of special interest to the members of this Society to know that for quantity and quality his Rhododendron collection is unique and

is easily the finest extant. Forrest was very devoted to this genus and was ever hoping to find the "centre of the Rhododendron world." Whether there is such a place I gravely doubt—unless it is defined broadly as Western Yunnan. But Forrest's contribution to the genus is as his memorial, something "more lasting than bronze." Primula probably came next in his affections and he made many notable additions to the known species.

I have already referred to some of the reasons which made Forrest so successful an explorer, but there are still some of his characteristics well worth recording. He shared very markedly in the attributes of the *naturalist* of the days before this era of specialisation. His collections of mammals, birds, and insects have been overshadowed by his botanical finds, but they were noteworthy in their way and he was much interested in securing them. He was full of information regarding the various peoples he came in contact with—their manners, customs, and pursuits. He knew much of the geological formations and minerals of the province, and his notes on plants generally included reference to the character of the soil. Long before it was admitted he knew that many Rhododendrons would grow on limestone.

He was singularly successful in the training of the native collector. These hillmen became remarkably adept and served the useful purpose of covering more ground than even his energetic self could hope to do. They were most loyal assistants. A cable from Forrest was enough to set them going and on his arrival at Bhamo he was welcomed by men who had in some cases journeyed six weeks to meet him. His seed-collections consequently were on a generous scale. He was even reproached sometimes for too catholic a taste in his choice of plants. It is easy to prophesy after the event, and no easy matter for a collector in the wild to interpret horticultural value. There are many Gentians in Yunnan which rival *G. sino-ornata*, but will they adapt themselves to our climate? There are many Primulas there transcending *P. malacoides*, but not one of them is likely to receive a similar welcome and attention from horticulturists throughout the world. There are glorious alpines on the cliffs of Yunnan such as *Isopyrum*, *Solms-Laubachia*, and *Lithospermum*, but have they been successfully introduced? Forrest went on the principle of securing all he could and so tried to satisfy both horticulturist and botanist. Members of the Society may be assured that from the scientific point of view the mass of material at different stages obtained by Forrest has proved of the utmost value in interpreting the many problems of their favourite genus.

Forrest had good powers of organisation and his explorations were carried out very methodically. He acquired a fair facility with that most difficult language Chinese, and some acquaintance with hill-dialects. An enthusiastic photographer, he was the possessor of some thousands of illustrations of the country, its peoples, and its plants. His photographic records of alpines show conclusively that, much as he relied on his men for the detailed collecting, he never spared himself his full share of hard work on the highest cliffs and screes. Among the noteworthy Forrestian plants I can recall only one or two which he himself had not seen *in situ*.

He was well acquainted, as he had to be, with the written records of the discoveries of his predecessors and was a persistent searcher after their more important and often elusive finds. One such, *Primula*

glacialis from the Lichiang, cost him long and almost vain pursuit—the book description was all he had to go by—and years after it was clear that he had secured it without its identity being realised at the time. The notes attached to his specimens are indicative at all times of keen observation, sound knowledge of the systematic position of each plant, and withal an eye for beauty.

It is a thousand pities that he could never be induced to write an account of his travels. The story of these last twenty-seven years would have been a fascinating one. Often spoken of, it was always postponed till his days of retirement—days which never arrived. The task did not appeal to him, and yet in his letters it was evident enough that he had the gift of narration. In many ways he was reserved and not a talker except in the company of his personal friends, and then he always held his own. Diffident of his powers of speech, he was not often persuaded to give a lecture. In his earlier attempts he was, in the parlance of the Scottish Church, a "reader," but in his later years he spoke with freedom and delighted large audiences, illustrating his story with numerous lantern slides taken from his own excellent photographs.

There was no mistaking the fine quality of the man and the evidence of power. He was in many ways a "bonny fechter." Sternly self-disciplined and eminently a man of his word, he was ever scrupulously anxious to do his best for those in whose interest he undertook his explorations. It is pleasing to record that in one of his last letters home he expressed himself satisfied with the spoils of 1931. *Ipsissma verba :* "I may with safety say that this will be the best year I have yet had. If all goes well, I shall have made a rather glorious and satisfactory finish to all my past years of labour." A true prophecy . . . but how gladly would his many friends have stayed the hands of fate, were it only for a little longer. *Ave et vale.*

TRANSACTIONS

OF THE

BOTANICAL SOCIETY OF EDINBURGH

SESSION XCVII

Stem Cuttings in Ephedra.

By R. J. D. Graham, M.A., D.Sc., F.R.S.E. (With Pl. III.)

(Read 16th March 1933.)

The usual method employed for increasing stocks of the species of *Ephedra* is propagation by means of seeds, divisions, or by layering (2). Ephedrine hydrochloride is obtained from an alkaloid present in various species of *Ephedra* (1), and this drug is at the present time attracting a considerable amount of attention owing to its employment in ophthalmology (4) and in the treatment of asthma and whooping-cough (6).

Plants containing alkaloids have been recorded as presenting problems to the propagator (7), while the presence of stereoms which are very fully developed in *Ephedra* (3) has been postulated as a possible obstacle to the easy rooting of cuttings (5). Opportunity to test these points was afforded by *Ephedra nebrodensis* and other species of *Ephedra* which grow freely out of doors in the Royal Botanic Garden, Edinburgh. Stem cuttings consisting of the terminal five or six nodes of the current year's growth were inserted in sand in a cold frame in February, while others were placed in sand in a cold pit. Callus formation proceeded in both cases, but root development was more rapid in the drier environment. Stem

cuttings were successfully raised in a month's time, thus providing a method of expeditiously and economically multiplying a stock of uniform composition.

The anatomical changes which occurred during propagation have been studied, and these are of interest because of the presence at each node of an intercalary meristem in addition to the fascicular cambium. The lignified pith which occurs in the centre of the stem portions used for cuttings is interrupted at each node. This interruption is due to a meristematic region which occupies the node and extends for a short distance upwards and downwards into the contiguous internodes. Above the node an extension of the upper layers of this hour-glass-shaped zone partially interrupts the vascular tissue, the connection of the xylem elements being maintained by short lignified elements. After crossing the vascular tract this extension of the upper layers of the meristematic zone is carried across the cortex to the epidermis.

Active wound callus formation takes place over the basal end of the cutting and in three weeks' time a massive cushion has formed over the cut surface. In the formation of this callus pad both the wood cambium and the nodal meristem have taken an active part. An arc of products from the wood cambium has extended inwards over the cut xylem and joined an arc of products derived from the nodal meristem which has developed outwards. The internodal stereoms are interrupted as the node is approached and consequently offer no barrier to callus extension outwards over the cortex.

The outer layers of the callus pad are suberised, but root primordia are initiated in the centrifugal products of the actively dividing region derived from the wood cambium and the nodal meristem. Root development is oblique to the cut surface and the roots make their appearance externally at an obtuse angle to the stem.

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(2) Bean, W. J.: Trees and Shrubs, i (1914).
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(4) Orr, H. Campbell: Practitioner, cxxii (1929).
(5) Reid, O.: Trans. Bot. Soc. Edin., xxviii (1923).
(6) Stewart, H. Hamilton: Brit. Med. Journ., i (1929).
(7) Stewart, L. B.: Royal Hort. Soc. Journ., lii (1927).

L.S. of stem cutting of *Ephedra nebrodensis* showing two proximal nodes; *a*, lignified pith; *b*, *b′*, meristematic region occupying node; *c*, wound callus formation; *x*, *x′*, arcs of products derived from wood cambium and nodal meristem; *r*, *r′*, *r″*, root initials (× 26).

R. J. D. Graham.

Hard Seeds and Broken Seedlings in Red Clover (*Trifolium pratense*). IV. Early Stages of Germination (Physical).

By Alexander Nelson and Jas. C. Macsween.

(Read 20th April 1933.)

On a resumption of the work on these seeds which, while appearing perfectly normal, fail to swell up with water and so remain hard, it was felt that the accepted ideas on the early stages of normal germination required checking. These early stages are almost entirely physical, and occur before respiration and other manifestations of life attain any intensity.

Red clover does not lend itself to the type of technique adopted, and so for the purposes of this research the Broad Bean (*Vicia Faba*) was chosen. *Vicia Faba*, so far as can be ascertained, never produces seeds showing any definite type of delay in germination and was selected for the work because of this inherent normality.

Material.—The material used consisted of a large sample (14 lbs.) of Broad Bean of variety "The Cropper," which originated from one plant and has been kept as a "pure line" by the raisers, Messrs David Bell, Ltd., who supplied the sample used.

Methods.—Individual seeds were drawn from the bulk, examined carefully for mechanical damage, disease, and other blemishes. Seeds passed as normal were weighed with great accuracy (to ·1 mg.) in the dry condition, then wetted by immersion in distilled water for a few minutes, taken out and surface-dried with a piece of well-boiled linen, and again weighed. The individual seeds were then placed in vessels containing redistilled water maintained at 20° C. in the dark, in a thermostatically controlled incubator. Periodically (every two hours) each bean was taken from the water, surface-dried and weighed, the weighings continuing for 48 hours. At each weighing the water in the vessels was changed in order to obviate as far as possible any effect of the seed on the water. Rudolfs (1922) has shown that germinating seeds

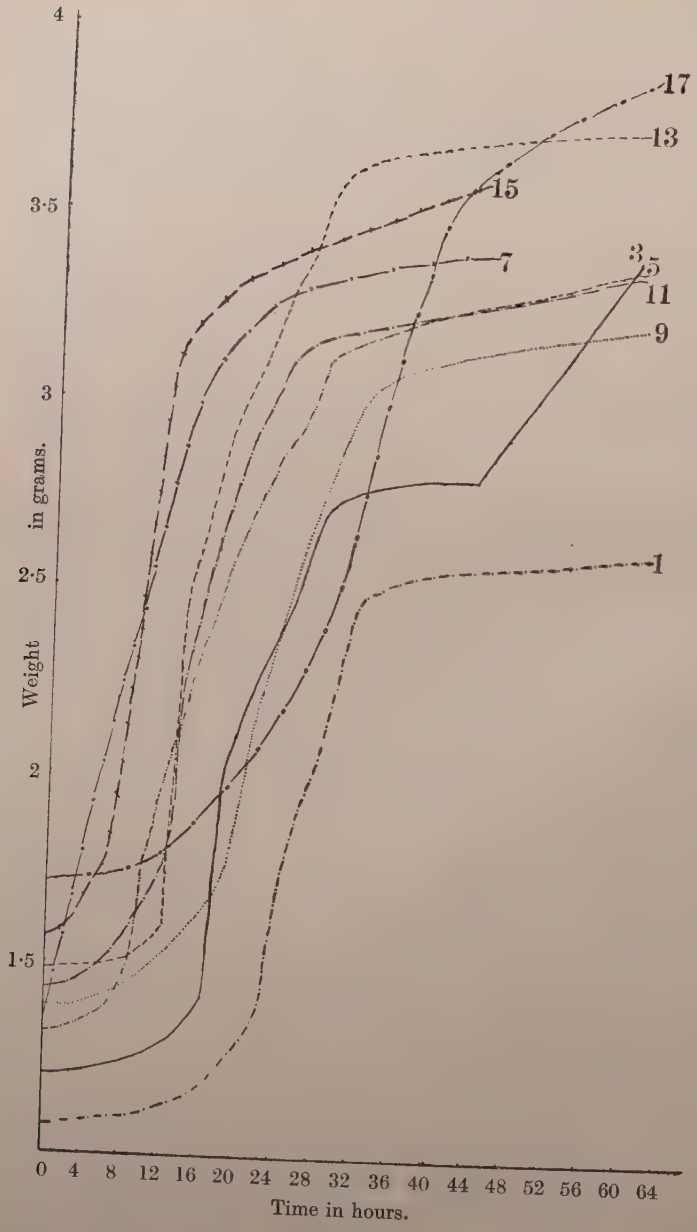
4
3·5
3
2·5
2
1·5
Weight in grams.
0 4 8 12 16 20 24 28 32 36 40 44 48 52 56 60 64
Time in hours.
17
13
15
7
3
5
11
9
1

Fig. 1A.

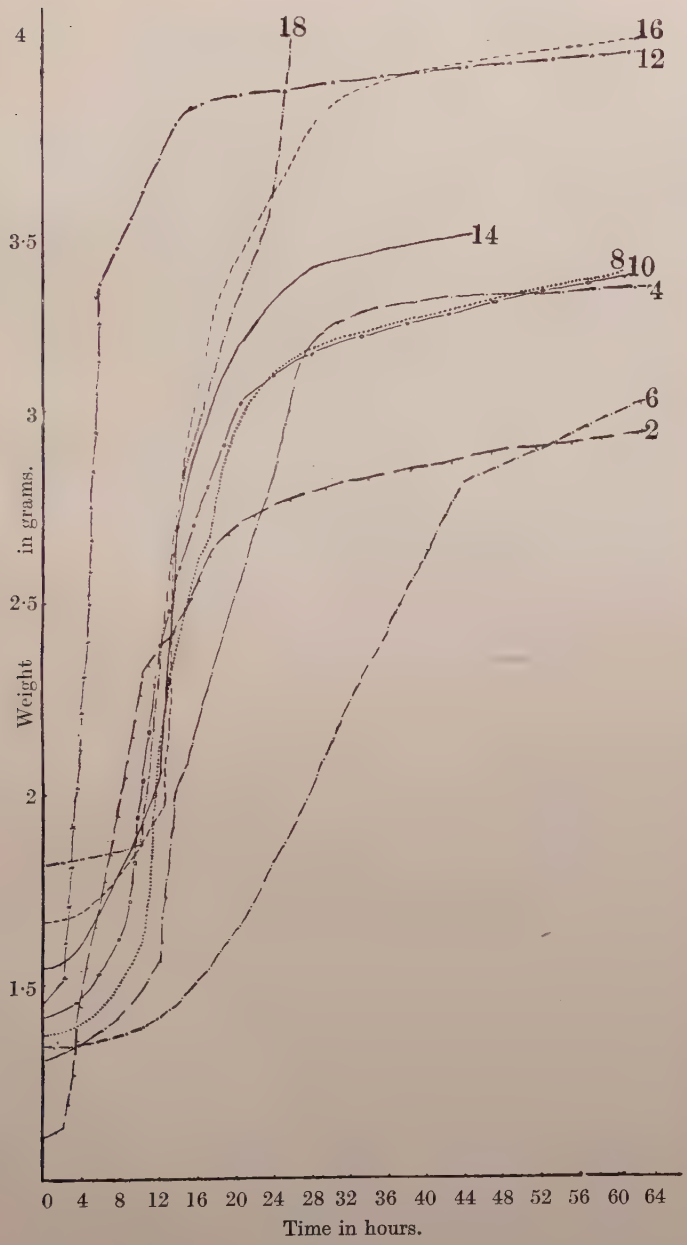
18
16
12
14
8
10
4
6
2
4
3·5
3
2·5
2
1·5
Weight in grams.
0 4 8 12 16 20 24 28 32 36 40 44 48 52 56 60 64
Time in hours.

Fig. 1B.

alter the hydrogen-ion concentration of the solution they are immersed in. It is not suggested that these conditions given to the seeds were "optimal," merely that they were stable.

Results.—Figs. 1A and 1B show the increase in weight of each of the beans plotted against time. The curves bring out the individuality of the seeds. For example, seeds 2 and 7 show a rapid initial rise compared with 1 and 9, which show a lag. The general shape of the curves is a simple S. It might be assumed that these curves deal with a smooth progression of events in a homogenous system. When the increase in weight for each period is plotted against time this picture of "smoothness" disappears. Such data are shown in figs. 2A, 2B, 2C. In these curves, while the individuality of the seeds tends to obscure the position, the definite "double maxima" shows that two mechanisms are involved. Other methods of treating the figures confirm that there are two mechanisms in the early stages of seed swelling.

A mechanism which is often considered to be responsible is that quoted in many text-books, the micropyle and hylar tissue. The anatomical investigation of this area has been well done by Pammel (1899) and his drawings have been checked. Careful observation of the "hylar split" showed that this aperture closes within 90 seconds after wetting, due to colloidal swelling of one layer working over another layer which does not swell. It thus appeared that the passage of water through a pore or split was unlikely. This was confirmed by supporting individual beans by "life-belts" of paraffin wax floating in distilled water under the general conditions already outlined for the whole bean. Twenty beans were floated micropyle downwards and twenty micropyle upwards. The increase in weight characteristics of both groups were similar and also essentially similar to the curve for increase in weight of the total bean. It may be assumed that the hylar end of the bean provides no mode of ingress for water different from the general surface of the bean.

One obvious mechanism of early intake is the hydration of the seed colloids and the fact that the testa increases in bulk in this way is evidenced by its wrinkling and folding shortly after immersion. This wrinkling disappears after a further period of immersion and free liquid appears between the testa

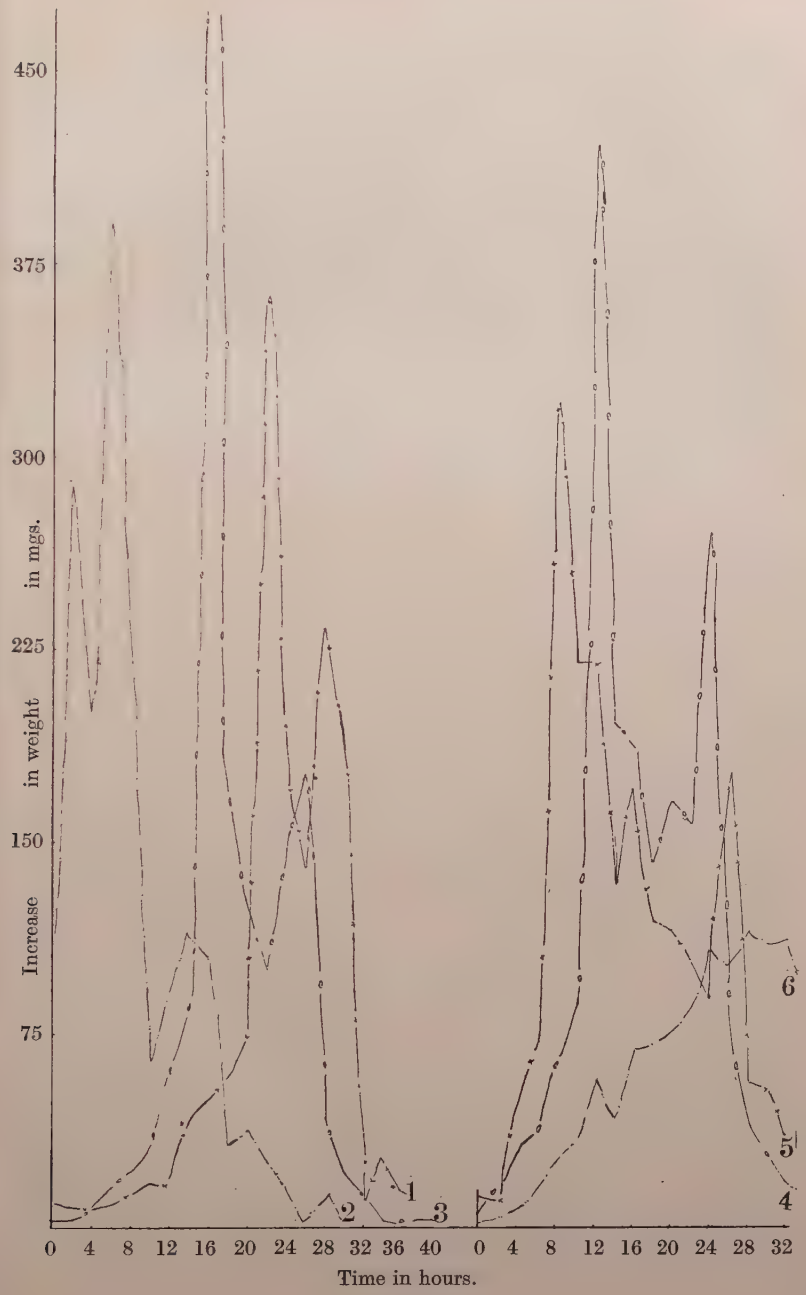
450
375
300
225
150
75
Increase in weight in mgs.
0 4 8 12 16 20 24 28 32 36 40
0 4 8 12 16 20 24 28 32
Time in hours.
1
2
3
4
5
6

Fig. 2A.

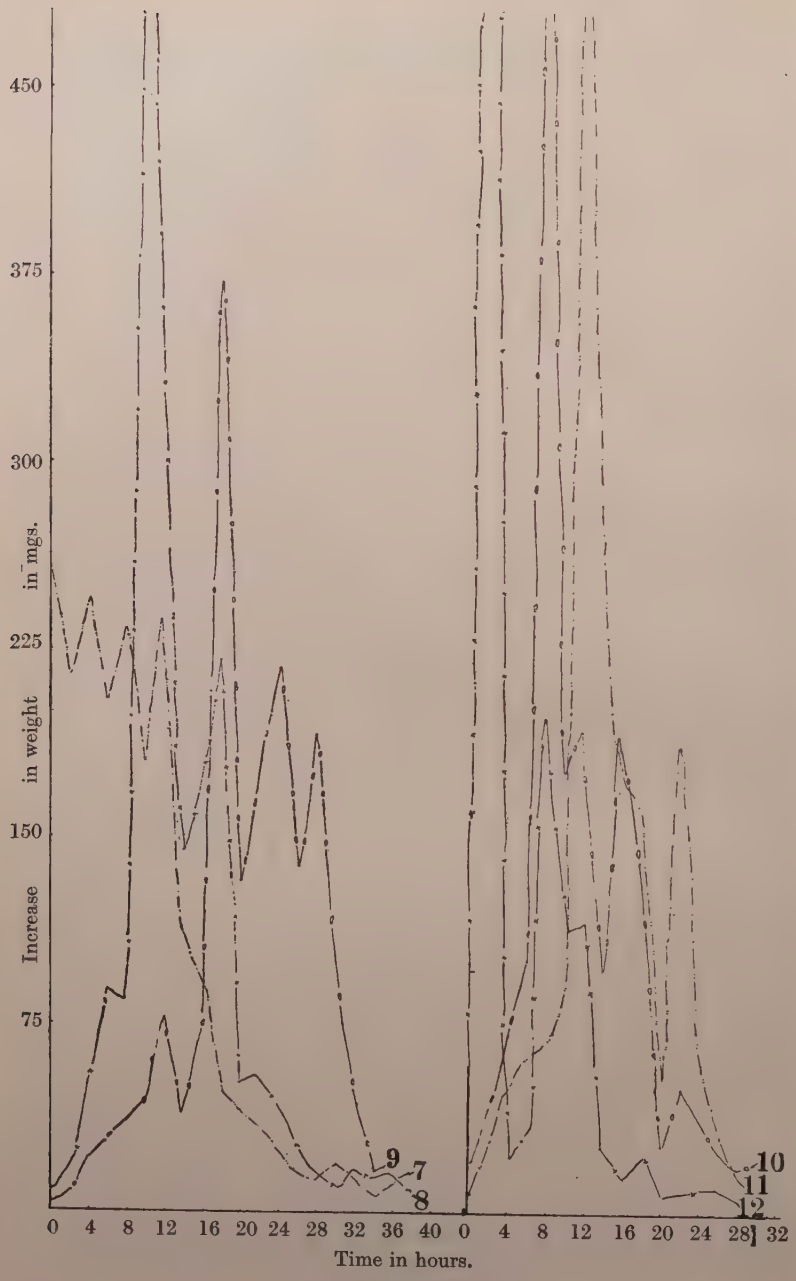
450
375
300
225
150
75
Increase in weight in mgs.
9
7
8
10
11
12
0 4 8 12 16 20 24 28 32 36 40 0 4 8 12 16 20 24 28 32
Time in hours.

Fig 2B.

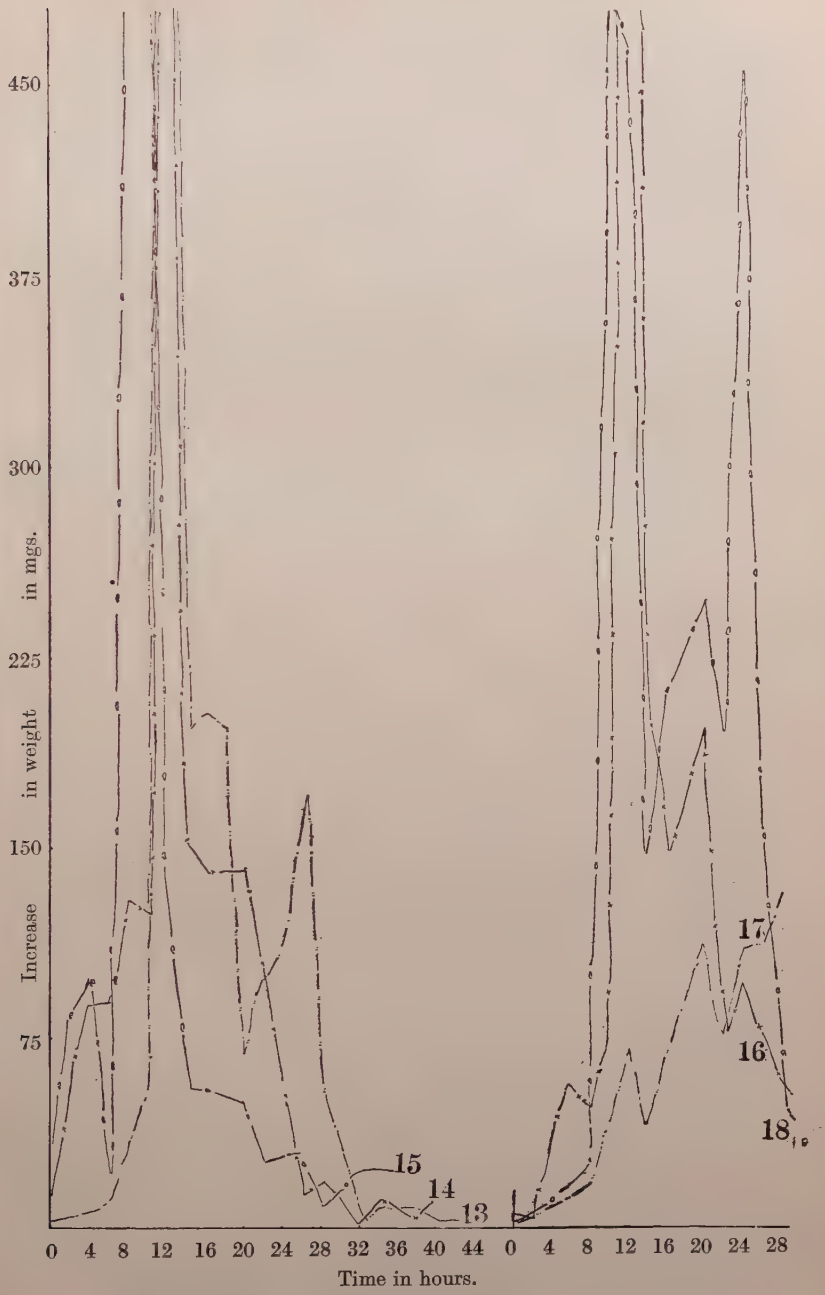
450
375
300
225
150
75
Increase in weight in mgs.
0 4 8 12 16 20 24 28 32 36 40 44 0 4 8 12 16 20 24 28
Time in hours.
13
14
15
16
17
18

Fig. 2c.

and the embryo proper. Shull (1913, 1920) has reported the testa of certain seeds as being of a semi-permeable nature, and this has been confirmed for *Vicia Faba*. Circular discs of the dry testa were cut with a specially made cutter to fit the apparatus shown in fig. 3. When the apparatus was placed in water and the portion of testa became wetted, liquid rose up in the tube. The source of the osmotically active substance was found to be located in the rather undefined layer lining the testa. The free liquid found inside the testa of a fully swollen bean reduced Fehling's solution, while tests for a reducing substance or for a carbohydrate (Molisch test) on the liquid outside the swelling bean proved negative.

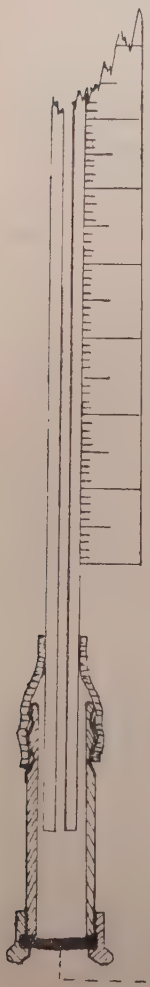

FIG. 3.
T = portion of testa.

A survey of the hydrogen-ion concentration of the bean tissues, using the range indicator method of Small (1929), showed that during the period discussed here all tissues remained remarkably constant except the layer of tissue between the testa and the embryo. This tissue dropped from pH 5·9 in the dry seed to below pH 4 in the swollen seed. It is suggested, then, that the second step in normal water intake by the seed of broad bean is osmotic in nature, due to the semi-permeability of the hydrated seed coat, and that the supply of osmotically active substance required to operate the mechanism is derived from the hydrolysis of carbohydrate located in the undefined layer of tissue internal to the testa and external to the embryo proper.

SUMMARY.

The mechanism of water intake by the seed of broad bean is not simple but involves at least two mechanisms. In

point of time the first is hydration of the colloids of the testa; this is followed by an osmotic intake of water through the semi-permeable membrane of the testa, the osmotically active substance being a reducing sugar formed from carbohydrate not in the embryo itself. The passage of water through apertures such as the micropyle or hylar slit is not significant if it takes place at all. These structures are probably concerned with ripening processes if they have any function after fertilisation.

It seems clear, too, that any detailed study of germination must take cognisance of the individuality of each seed. This individuality may be conditioned by many factors other than genetical; hysterisis effects in the colloids following on different histories of harvesting, period of development at harvest, drying after harvest are obvious factors. Different content of carbohydrate in the layer below the testa must affect the second (osmotic) mechanism.

The balance necessary for this work and the thermostats used were purchased with a grant from the Moray Fund for Research of Edinburgh University.

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Vegetative Propagation in Cotoneaster. By William A. Clark, B.Sc. (With Pls. IV–V.)

(Read 18th May 1933.)

Prostrate shoots of *Cotoneaster microphylla* generally root if left to themselves, the roots appearing from the under-surface of the stem which is in contact with the earth. The roots appear just above the emergence of a bud and are found in regular sequence up the stem (Pl. IV, fig. 1). For ease of control, stem cuttings were employed in the following experiments. The cuttings were taken from 1- to 2-year-old wood and were struck in (1) bulb fibre, and (2) sand in a flower-pot plunged in fibre in a propagating frame. The day temperature in the propagating frame was maintained at 70° F.

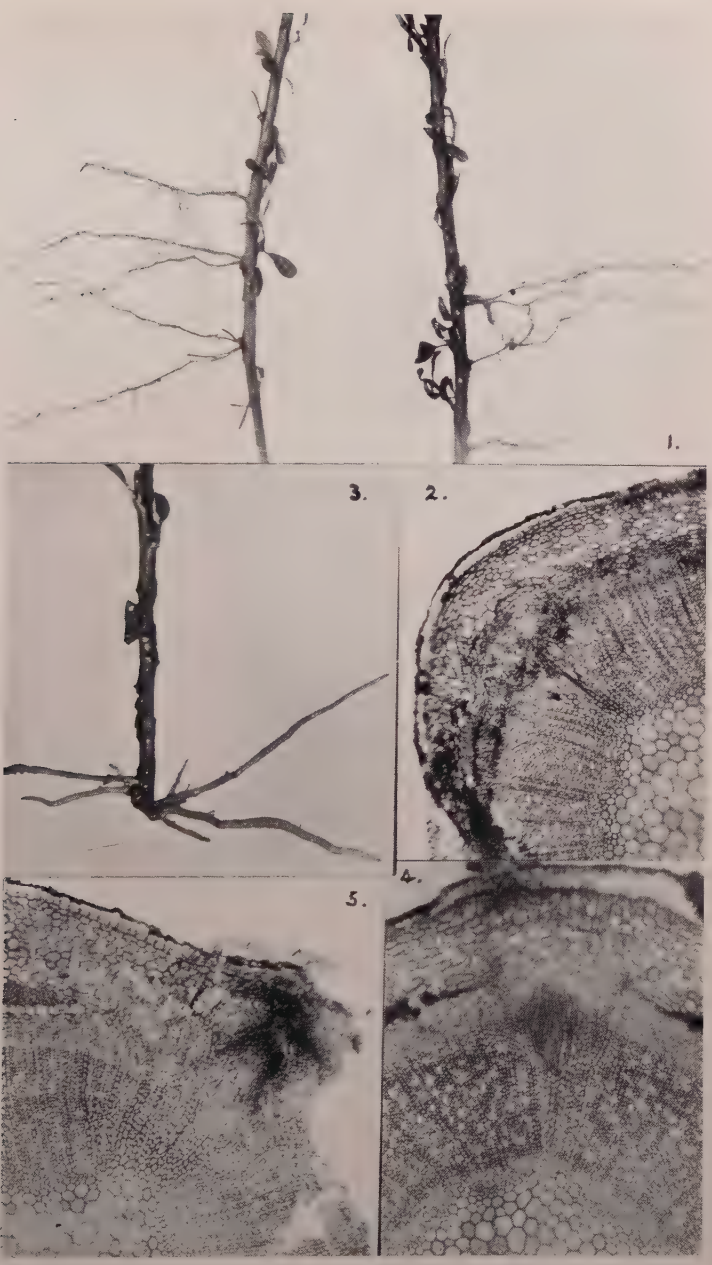
Methods.—Sections were cut without previous embedding with a sliding microtome; they were supplemented by hand sections wherever possible.

The fixatives were formalin acetic alcohol (Chamberlain (1)) and 90 per cent. alcohol.

The stains used were an alcoholic solution of safranin (strength of alcohol 50 per cent.) followed by one of the following stains: aniline blue 1 per cent. solution in clove oil, and Delafield's haematoxylin.

Root Initials.

Root initials must be regarded as part of the normal anatomy of the stem as they are always found present in the stem. In the older parts of a normal upright stem, a slight protuberance is noted above practically every axillary bud. These protuberances are associated with a closing bud gap; as many as 3 and 4 have been noted in the same gap. No protuberances are seen in the current year's growth, and this would seem to indicate that root initials are initiated, if not during the second year's growth, at least towards the end of the first year's growth.



WILLIAM A. CLARK.

Growth and Structure of Root Initials.

After initiation further root growth is inhibited or at least is only sufficient to keep up with the secondary thickening of the stem. In other words, they are dormant or latent.

After the production of such a root initial, further development is only brought about by natural or artificial layering of the branches. The photograph (Pl. IV, fig. 1) shows, on a portion of a stem, adventitious roots produced as a result of natural layering of the stem. Further development of root initials can also be brought about by isolation of a portion of a stem—that is, by making a cutting.

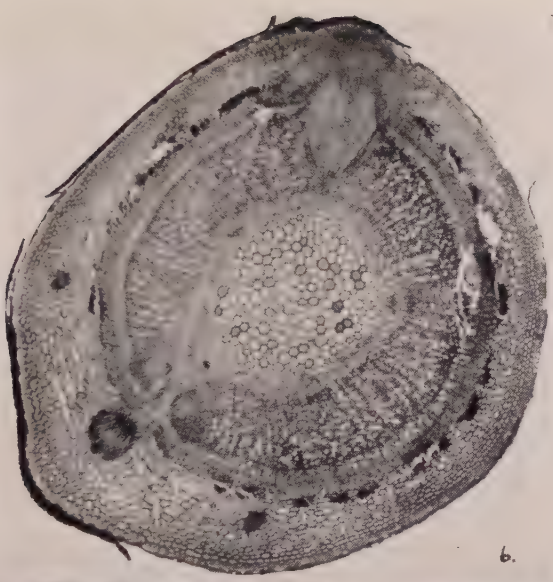
Observations, made in regard to the production of roots on cuttings, showed that the production of roots varied with the seasons of the year. Cuttings were inserted in the frame at regular periods between October 1932 and March 1933. Of those inserted in October, November, and December, the number of cuttings giving rise to roots was very small. In those which did root, the roots took on an average 18 days to burst through the stem. It is interesting to note, however, that these cuttings planted in October, November, and December produced a large amount of callus, the first signs of which were seen in 5 days. Those planted in January 1933 showed an increased number of cuttings producing roots although the number was still relatively small. In February and March, however, roots were produced in nearly all the cuttings planted, and they took 14 days to burst through the stem. Roots $1\frac{1}{2}$ inches long were obtained in 24 days (Pl. IV, fig. 3). However, in these cuttings taken in February and March very little callus was formed and 10 days elapsed before the callus was noticed. Comparing this with the cuttings inserted in October, November, and December it would seem as if callusing and rooting are negatively correlated and that successful rooting depends on little callus formation.

To determine the internal structure, the exact position of the root primordia and also the tissue from which they arise, transverse and longitudinal sections of them were cut before they had burst through the cortex. The primordia could easily be distinguished as slight protuberances just above a leaf insertion.

Transverse sections through primordia revealed the fact that the adventitious roots occurred in a closing bud gap (Pls. IV–V, figs. 2, 4, 6, and 7). Although no definite indications have been found of cambium bridging the gap, some signs are not wanting that such an occurrence may take place. The earliest stages of root formation show the bud gap to contain a mass of meristematic cells (Pl. IV, fig. 2). The cells constituting the meristematic mass are more or less isodiametric in shape, although the radial axis may be slightly longer than the tangential axis. They must have been formed by radio-longitudinal and transverse divisions of the initial meristematic cells. The nuclei of these cells are large and spherical with a diameter of 5 μ. It was noted that the cambium at the edges of the bud gap shows increased activity. It could not be definitely determined whether the meristematic group of cells occurring in the bud gap is the result of the activity of the cambium, or whether the activity of the cambium is due to the presence of meristematic cells in the bud gap. It would seem likely that the former is the more probable. In connection with this it is interesting to note that the cambium of the vascular cylinder of the stem is in continuity with that of the root initial (Pl. V, fig. 7).

From external evidence already presented it is postulated that these primordia are initiated at the end of the first or during the second year. This would mean that the meristematic group of cells giving rise to the root initial must have been initiated in the bud gap at the end of the first year. This is further borne out by the evidence from transverse sections. In sections of 1-year-old wood no signs of primordia nor of any meristematic tissue were seen in the bud gap. Sections of root primordia showed that they had been initiated at the end of the first year because the first formed wood elements of the root initial coincided with the first annual ring of the stem (Pl. IV, fig. 4).

Once initiated, the mass of meristematic cells divides actively and the resulting increased number of cells arches out of the bud gap into the cortex. It now constitutes a meristematic cone of cells (Pl. IV, fig. 2). Differentiation soon takes place in this meristematic cone. The cells to the interior of the cone become elongated and vacuolated; those to the exterior of the cone increase in size, vacuolate, and form an outer layer.



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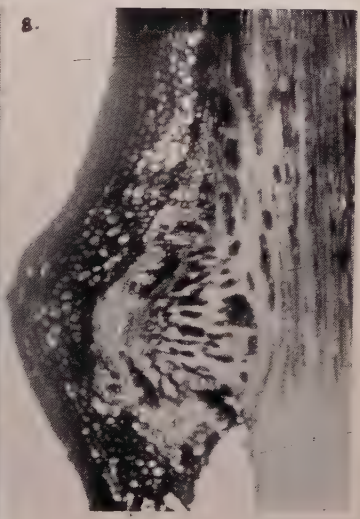


As the root pushes its way to the exterior, the cortical cells in its path are crushed and pushed before it, forming a protuberance which is noted before the root actually emerges from the stem.

Vascular elements must be formed very early in the root initial, as in nearly all the primordia sectioned, vascular tissue was present.

Transverse sections show that the vascular elements of the root initial form a wedge-shaped structure partially filling the leaf gap and thus appearing embedded in the vascular cylinder of the stem (Pl. V, figs. 6, 7, and 8). The broad end of the wedge is exterior in position and the point tapers away towards the pith. This wedge-shaped structure is apt to prove misleading if the nodal anatomy of a normal stem has not been previously studied as it is difficult to understand how this wedge could be pushed into the vascular cylinder.

At the node a depressed segment is found after the emergence of a bud. The meristematic tissue which gives rise to a pre-formed root initial, and which occurs in the bud gap, is therefore also depressed. The cells in the centre of the meristematic tissue now become elongated radially. Sliding growth takes place in these cells followed by differentiation into wood elements. Sliding growth is only partially responsible, however, for this wedge-like appearance of the vascular tissue of the root. Secondary growth of the stem is the other factor involved. Linking these wood elements, produced by sliding growth, to the vascular elements at the sides of the gap, are oblique tracheids whose end walls are applied to the sides of the vessels in the stem (Pl. V, fig. 7). They have been produced from the actively dividing cambium, noted previously, which occurs at the edges of the gap.

Now as secondary thickening takes place in the stem, a corresponding increase in length must take place in the root or it would be engulfed in the xylem cylinder. This does take place, new tracheids being formed from the centre of the meristematic cone which are again linked up by oblique tracheids to the newly formed secondary wood elements of the stem. As long as the root initial remains dormant this process continues, so that the base of the root becomes embedded in the xylem cylinder of the stem and produces the wedge-shaped structure previously described.

The vascular elements of the wedge are composed of tracheids and wood parenchyma. The former average 77 μ in length by 14 μ broad. Scalariform, reticulate, and pitted tracheids are observed. The wood parenchyma elements are smaller and contain large numbers of starch grains; they are also pitted.

The base of a vascular system so produced is therefore seen to be embedded in the vascular cylinder of the stem and in fact incorporated within it (Pl. V, figs. 6, 7, and 8). This partial embedding of the first-formed root tracheids in the bud gap and subsequent secondary xylem formation afford a very strong means of attachment of the adventitious root to the stem. Also, as these newly formed tracheids are early in communication with the vascular elements of the stem, a supply of food material is assured for the actively dividing meristem.

On propagation, the meristem of the root initial shows a marked increase in activity, rapid division of the apical cells taking place. New tracheids and vessels are formed, linking up with the pre-existing ones. In 14 days the root has burst through the stem and in 24 days roots $1\frac{1}{2}$ inches long are produced (Pl. IV, fig. 3). The cambium at the base of the roots also divides actively, forming wood elements inwards. The vessels of the root show spiral thickenings.

This work was carried out at University College, Dundee, and the writer acknowledges his indebtedness to Dr. E. Philip Smith for her constant advice during this investigation.

Summary.

1. Pre-formed root initials are found in *C. microphylla* and are seen as slight protuberances above the emergence of the bud. These root initials originate as a group of cells in the bud gap. As sections of old root initials show the vascular cambium of the stem to be in continuity with the apical meristem of the root initial, it is very probable that the root initial has been produced from the cambium of the stem.

2. The wood elements of the root initials become embedded in the bud gap of the stem, due to secondary growth of the stem and sliding growth. They form a wedge-shaped structure.

3. On propagation, roots are produced by a resumption of growth of the pre-formed root initials.

4. Cuttings were inserted in the frame from October 1932 to March 1933. Those in March rooted most successfully.

5. There is a negative correlation between callusing and rooting.

Reference.

(1) Chamberlain, C. J.: Methods in Plant Histology, 4th revised edition (1928).

EXPLANATION OF PLATES.

Cotoneaster microphylla.

Fig. 1. Rooting of natural layer.
Fig. 2. T.S. stem to show earliest stage of pre-formed root initial obtained. ×45.
Fig. 3. Rooted cutting.
Fig. 4. T.S. stem showing older pre-formed root initial. Note position of initial in relation to annual ring. ×45.
Fig. 5. T.S. stem to show root initial induced after fifteen days in the propagating frame. ×45.
Fig. 6. T.S. stem showing old pre-formed root initial with wedge-shaped xylem embedded in vascular cylinder of the stem. ×25.
Fig. 7. T.S. stem, same as fig. 6. The apical meristem of the initial is in continuity with the cambium of the vascular cylinder of the stem. ×45.
Fig. 8. L.S. stem showing pre-formed root initial. ×45.

The Nodal Anatomy of Spartina Townsendii.

By Isabel Lauder-Thomson.

(Read 15th June 1933.)

While studying the general anatomy of *Spartina Townsendii* a thorough examination was made of the nodal plexus.

To make this quite clear it was found necessary to construct a three-dimensional model of the vascular anatomy of the node of the culm. Although this was done on a fairly large scale it was found necessary to omit the smaller bundles.

From the model and from a series of microtome sections the anatomy of the node was made out.

The Node of the Culm.

No buds or adventitious roots were present on the mature nodes used for examination. Seventy-one bundles varying much in size occurred in the internode below the node used for the construction of the model. These bundles can be treated in four groups as they enter and leave the nodal plexus.

Firstly, there are thirteen bundles (eleven placed centrally) which form the main bundles of the next foliage leaf; these will be called the *first leaf bundles*. Alternating with these, slightly farther from the centre, is a set of smaller bundles which will be called the *second leaf bundles*. The third set of bundles constitute a ring surrounding the first and second leaf bundles. These abut on the stereome of sclerenchyma, and will be called the *cauline bundles*. Finally, there is a ring of very small bundles situated in the tissue separating the subepidermal air spaces. These will be named *subepidermal bundles*.

It will be shown that each of these four sets of bundles has a special rôle, and although there are complications due to branching and anastomosing of bundles, these are only minor occurrences which tend at first to distract attention from the main plan.

The development of the nodal plexus begins first on the side of the stem from which the overlapping edges of the leaf

sheath arise. This part is further complicated by a double supply of leaf bundles.

The First Leaf Bundles.—These bundles are situated centrally in the stem below the node, except for two which appear in an outer ring of bundles. The central ring of first leaf bundles gradually moves inwards at the plexus and then rapidly outwards into the leaf sheath. During their course the bundles gradually increase in size from 200 to 220 μ by 150 to 190 μ below the node, to 300 to 350 μ by 180 to 300 μ in the node. As they pass to the leaf sheath they rapidly diminish until they become from 90 to 100 μ by 70 to 90 μ.

The aberrant first leaf bundles are smaller than the others, and are destined to form the larger marginal bundles of the leaf sheath. These two, unlike the rest of the first leaf bundles, do not increase greatly in size.

As the first leaf bundles enter the node a few connections arise between them and the cauline bundles, these, however, soon break down.

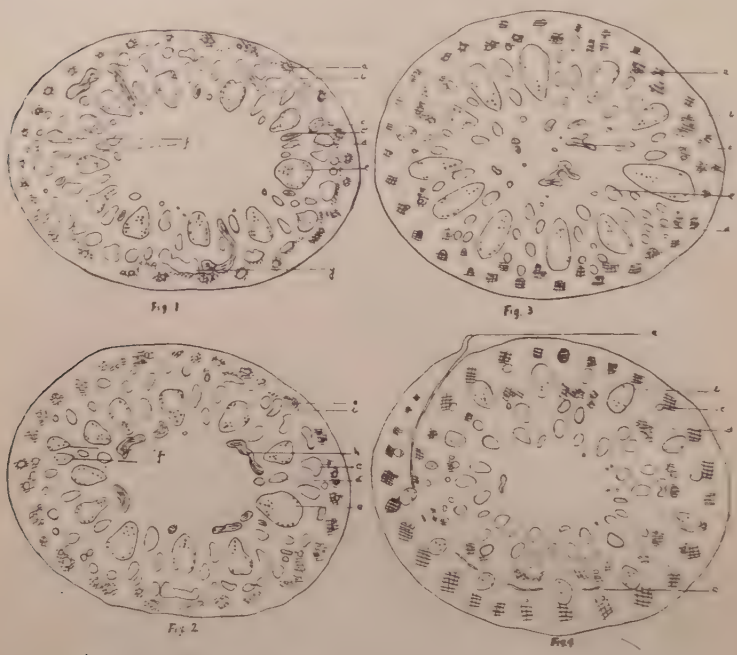
The Second Leaf Bundles.—These bundles are situated between the first leaf bundles, but their position is not so central. In their early course they may give off small twigs. In nearly all cases temporary connections are made with the branches of the cauline bundles which push into the middle of the stem. At the reduction of the plexus these second leaf bundles again form temporary connections with the branches of the cauline bundles which pass from the pith to the subepidermal tissue.

In the internode above, the second leaf bundles form the innermost ring, indicating that they will become the first leaf bundles of the next node.

The Cauline Bundles.—These form an outer ring of bundles, slightly smaller than the leaf bundles. They send forward branches between the first and second leaf bundles. These branches, as has been stated above, form temporary attachments with the second leaf bundles, but soon resume their individuality. When these branches reach a more central position than the first leaf bundles, lateral connections arise between them, which send forward twigs to form the network of the solid node (fig. 2). On the reduction of this network the twigs pass out again, forming temporary connections with the second leaf bundles and joining with the cauline bundles

or with the branches of the cauline bundles, which will be described below.

Having given off the nodal branches, the cauline bundles, by horizontal branching, form a "vascular wall" outside the



FIGS. 1 and 2.—T.S. of node of culm, ×14. (Camera lucida.)

a, subepidermal bundle; *b*, sclerenchyma; *c*, cauline bundle; *c'*, branch of cauline bundle moving in; *d*, second leaf bundle; *e*, first leaf bundle; *f*, aberrant first leaf bundles; *g*, beginning of "vascular wall"; *h*, cauline bundles forming lateral connections.

FIG. 3.—T.S. of node of culm, ×14. (Camera lucida.)

a, subepidermal bundles and sclerenchyma forming two rings; *b*, first leaf bundle; *c*, nodal plexus; *d*, cauline bundle; *e*, second leaf bundle.

FIG. 4.—T.S. of node of culm, ×14. (Camera lucida.)

a, outer margin of leaf sheath; *b*, first leaf bundle with sclerenchyma; *c*, subepidermal bundle forming smaller bundle in leaf sheath; *d*, subepidermal bundles of next internode; *e*, division between first leaf bundles.

leaf bundles. This extends for a short distance and then is resolved into many small bundles which gradually anastomose and pass inward (fig. 3). A number of branches which pass in more rapidly and take up a position between the first leaf

bundles and the second leaf bundles will become the second leaf bundles of the next node.

The Subepidermal Bundles.—These bundles are very small, situated in the tissue separating the subepidermal air spaces, which gradually disappear in the node. The small bundles begin to branch, small twigs passing inwards and joining the cauline bundles. As the nodal plexus is reduced large masses of sclerenchyma appear round these hypodermal bundles (fig. 3). Gradually, by the anastomosing and the splitting again of these bundles, two rings of bundles are produced. On the side where the overlapping edges of the leaf will be cut off the outer ring of bundles again splits so that it is double at this place (fig. 4). This outer ring is made up of bundles, each connected with a large mass of sclerenchyma. Alternating with these are masses of sclerenchyma without bundles, or with only a minimum amount of vascular tissue. This sclerenchyma will join the first leaf bundles as they pass outwards into the leaf tissue to form the larger bundles of the sheath and blade. The inner ring of subepidermal bundles, with the connected sclerenchyma, form temporary connections with the cauline bundles. They then split up and form almost a complete ring round the stem. Gradually they anastomose again and take up a position in the tissue separating the air spaces in the new internode.

The Delimitation of the Leaf Sheath.—An interesting, though unimportant, point has been noticed. The leaf sheath begins to split off before the leaf bundles have passed into it. Divisions arise between the large vascular bundles, and do not join up until the bundles have passed well into the tissue of the leaf sheath (fig. 4).

Amphivasal Bundles.—Amphivasal bundles were observed in the nodes of *S. Townsendii*. These are very commonly found in the nodes of grasses. The first leaf bundles of *S. Townsendii* rapidly become amphivasal as they pass into the node and remain so until they begin to pass into the leaf sheath. Scattered spiral xylem elements appear on the outer edge of the phloem. This condition is not produced by anastomosis of bundles. No other bundles except the first leaf bundles were observed to become amphivasal.

The Node of the Rhizome.

In the rhizome the arrangement of the bundles is not the same as in the aerial stems. Proceeding upwards to a node

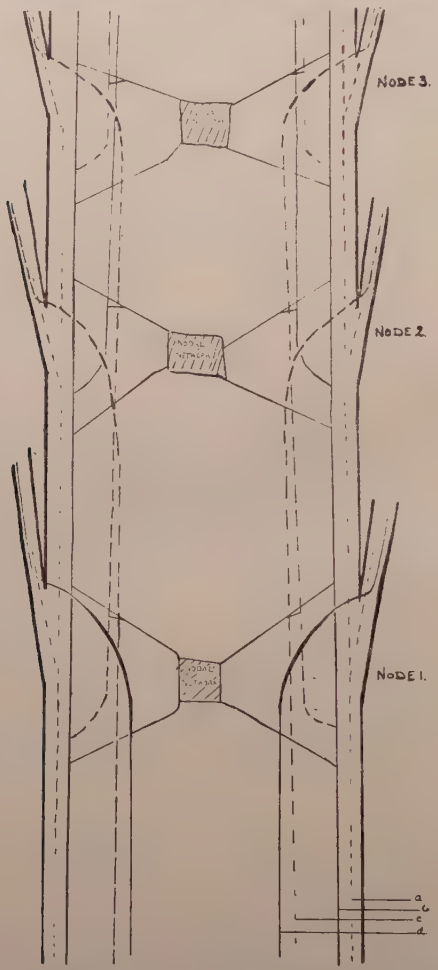


Fig. 5.—Showing course of the bundles in the stem.

a, subepidermal bundle
b, cauline bundle
c, second leaf bundle
d, first leaf bundle
} of node 1.

the central and outer air spaces gradually become filled up with the stellate tissue. As soon as the node is solid the

bundles of the scale leaf begin to pass out. The subepidermal tissue destined to form the scale leaf receives bundles alternately from the outer and inner rings. These bundles move across the stellate tissue and take up a position below the epidermis. There is a very simple nodal network; only three or four bundles from an inner ring send out branches into the pith.

The scale leaf is gradually delimited as the bundles pass into it. The splitting process, as in the foliage leaf (described below), seems to be held up by the outward passage of the bundles.

Soon after the scale leaf has split away, the stellate tissue breaks down again and a hollow pith is formed. Parenchymatous strips again appear separating the subepidermal air spaces. Meanwhile the bundles of the outer ring divide up and form a "vascular wall" enclosing the two inner rings. Finally this anastomosis breaks down and a ring of bundles similar to that present below the node is reconstituted. Similarly the inner two rings of bundles divide up, connecting one with another by lateral branches. They finally divide up and the inner two rings are reconstituted.

In the case of the rhizome both roots and buds were present.

Passing upwards from the internode, the roots appeared as soon as the node began to get solid. These roots were supplied by the bundles from the outer ring. A bud was present in the axil of the scale leaf. This was supplied by bundles from every ring; these appeared to move out simultaneously and arrange themselves in the young tissues.

Discussion.

Comparing the work on the node of the culm of *S. Townsendii* with that described by Arber (1) on *Phalaris arundinacea* and *Avena barbata*, the arrangement and movements of the bundles, although not identical in the details, are on the whole very similar. Arber describes four sets of bundles which supply the same tissues as those in *S. Townsendii*.

Percival (2) figures and shortly describes the nodal plexus in the wheat plant. Again the main scheme of arrangement agrees with that of *S. Townsendii*.

It would appear, then, that there is one plan on which the bundles are arranged in many grass nodes.

From the work undertaken it has been shown that the plexus is not connected with either the bud or the roots (fig. 5).

The nodal network can be considered as either cauline or foliar. If the so-called "cauline bundles" are really an aggregation of leaf bundles, then all the vascular bundles of the stem are foliar. If, however, there is a portion of each cauline bundle which always remains cauline, then the nodal plexus is truly cauline in origin.

Whichever way this may be interpreted, it is quite clear that the bundles passing to the first, second, and third leaf above, take no part in the plexus.

References.

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(2) Percival J.: The Wheat Plant, London (1921).

Abnormal Larch Cones. By M. Y. Orr.

(Read 15th June 1933.)

Proliferation of conifer cones is by no means an uncommon phenomenon, and a highly complicated structure is often produced as a result of exuberant growth. In some cases it is difficult to account for the particular form which the abnormality has taken, but in others there is the suggestion of a harking back to an ancestral type, and the anachronistic features displayed may then be utilised to interpret the precise nature of the constituent parts of a normal cone. By such means have morphologists endeavoured in the past to trace the phylogenetic history of the development of the cone in the Coniferae. It is not intended in this brief communication to comment upon the various hypotheses that have been founded on such teratological data, save in the case of such as seem apposite, but merely to describe an extreme case of proliferation in a larch cone, which was sent to the writer some months ago by Mr. H. A. Latham, Edinburgh, to whom due acknowledgment is now made.

The specimen in question (fig. 1) was taken from a tree growing in a garden at Appin, Argyll, and resembles a vegetative shoot but for the numerous small protuberances, most of them bifurcated, which occur in the axils of the lower leaves. An examination of these outgrowths disclosed the fact that each was actually an ovuliferous scale, bearing on its adaxial surface two minute ovules, complete in every detail, but situated a little farther apart than in a normal cone, owing to the partial bifurcation of the supporting scale. It was evident from this that the specimen was virtually a cone, despite its branch-like appearance, the resemblance to a vegetative shoot having been enhanced by the transformation of the bract-scales into foliage-leaves, each with several lines of stomata.

The production of leaves in place of bracts is not a very unusual form of reversion in the cones of conifers, and the more interesting point about this abnormal specimen is the tendency

of the ovuliferous scales to become divided into two divergent lobes, resembling fleshy leaves.

So long ago as 1842 Alexander Braun first formulated the theory that the ovuliferous scale represents the two first

FIG. 1.—1. Larch cone, showing an advanced stage of proliferation; 2. Ovuliferous scale of proliferating cone, under side; 3. The same, upper side, showing ovules; 4. Partial proliferation of a larch cone. (Del. B. G. Watts.)

transversely placed leaves of an axillary shoot, which have become fused along their margins to form a compound structure. Velenovsky has also recorded cases of proliferation in larch cones, where axillary shoots were produced, which bore, in addition to the two fleshy ovuliferous leaves mentioned by Braun, a number of similar leaves, each with an ovule attached. In the specimen which the writer is describing only the first pair of fleshy leaves is represented in the axil of each

metamorphosed bract, and although their disassociation is incomplete, there is sufficient indication of incipient dialysis to show that the abnormality is essentially similar to that referred to above.

It may be objected that such an abnormal specimen as that described can scarcely be said to belong to the same category as a cone, for the prolongation of the axis as a vegetative shoot, the replacement of the bract-scales by foliar organs, and the dwarfing of the ovuliferous scales point rather to a subordination of reproductive potentialities to vegetative activity.

By way of contrast to such an extreme case of proliferation a figure is included of a larch cone (taken from the same tree), which, despite the resumption of vegetative growth at its apex, still maintains the semblance of a cone (fig. 1, 4). The production of a few foliage leaves at the distal end of the cone-axis represents the limit of the proliferation in this case, and apparently there has been little or no diversion of nutritive substance from the purely reproductive parts. It is conceivable that the fertility of this particular cone would not have been impaired by such a minor proliferation, and, had it been allowed to mature on the tree, in all probability it would have produced a normal supply of seed.

The Root System of Acanthus. By A. McMartin, B.Sc., Ph.D.

(Read 15th June 1933.)

Acanthus montanus, a native of tropical Africa, is an evergreen shrub with unbranched, rather weak stems, and prickly leaves. A notable feature of the plant is the copious production of aerial roots, which are produced on the stem from below upwards to within the top few internodes. These have previously been described as stilt roots or prop roots. Schimper (7) says that "the stilt roots which give *Rhizophora mucronta* such a peculiar appearance occur relatively strongly developed elsewhere only in the herbaceous *Acanthus*." The term "stilt root" conveys the impression that the roots are produced by the plant to give support to a stem unable to support itself.

Examination of any plant, under cultivation at least, is sufficient to cast doubt over this assumption: these roots are obviously much too slender and lacking in strength to act as supporting organs; in fact, if the plant has to be maintained in an upright position, it has to be staked, notwithstanding the fact that the stem may be well furnished with these appendages.

While it is not denied that these organs when produced in sufficient number might assist in keeping a somewhat lax stem off the ground, the primary reason for their production must be assigned to some other cause. A significant fact in this connection is the lack of secondary growth in thickness of the stem. Examination of any stem reveals the fact that from the top few internodes downwards no increase in diameter has taken place. This, which will be referred to again, is due to lack of cambial activity and hence absence of secondary conducting tissue; a want which must be compensated for as the plant increases in size, and it is suggested that the method by which this want is overcome is by the production of these aerial roots, in the same way as Palms and other species lacking in cambium have overcome a similar difficulty.

This view is supported if one compares the habit of the plant

with its chief anatomical features. These are mainly a lack of secondary tissue production in stem and root, the retention in the latter of a relatively large pith for a considerable period, and the persistence of the cortex, periderm production, where occurring, taking place in the outermost cortical layers. These features are all those of a typical herbaceous plant, but nevertheless *Acanthus montanus*, as cultivated at least, does not show the typical herbaceous habit in that the aerial parts do not die down each year. (It is to be noticed that Schimper (7) refers to *Acanthus* as being herbaceous, but unfortunately does not say which species is referred to, as other species very closely related to the one under consideration behave as true herbaceous perennials.)

Assuming, then, that the acquisition of a herbaceous anatomy has provided the plant with a conducting system insufficient for its growing needs, the production of aerial roots is understandable as a response to supply this deficiency; and the purely mechanical concept of these roots being produced as struts must take a secondary place. That they have undoubtedly also a mechanical function is seen by their anatomy, which differs from the soil root, or soil portion of an aerial root after it has penetrated the substratum, in the more peripheral position of the conducting system and the relatively greater production of a strengthening tissue. This difference is shown more clearly if old roots be compared, when it is seen that in the soil root the conducting system is a central core, while in the aerial root a large pith is present. In fact, a transverse section of an old aerial root is more like that of a stem than of a root, a fact which is recognised in other aerial roots, e.g. *Pandanus* and *Rhizophora*. While this difference has without doubt a mechanical value, it will be shown that in *Acanthus* in the first place the difference can be traced to the root tip, where it is produced as a response to environmental factors which are probably nutritive in nature, and from which it follows that any value the difference in construction has to the plant from the mechanical point of view is secondary rather than primary.

The Root.

The aerial root is green, except for a region behind the root tip, and is covered with a dense mass of hairs giving it a felty

appearance. Branching never occurs except as a response to injury. Lenticels are present. As has been pointed out before, the general anatomical configuration of its tissues more nearly approaches that of a stem than a root. Starch grains are rare, but mucilage is abundant, especially at the tip.

The soil root is a branched, fleshy organ with a large reserve of starch and also contains mucilage. The conducting tissue is more centralised than in the aerial root. Externally this root is provided with a persistent covering of root hairs, which are dense in the older parts and, as in the aerial root, present a felty appearance.

Ontogeny of the Soil Root.—The following account of the ontogeny of the adventitious root of *Acanthus* produced in the soil is based on a series of transverse sections taken at intervals from the apex backwards in roots of various lengths. The length of these intervals and the lengths of the roots examined will be given when necessary. Before emergence from the parent organ the root shows internal differentiation into plerome, periblem, and dermatogen with root cap: these layers are distinct except at the apex, where, as will be shown later on, intense and uniform cell division in all three has resulted in their non-stratification. When the root is from 5–8 mm. long, the plerome gives rise to an embryonic pith and a procambium in which differentiation of stelar tissue commences immediately. The pith has a diameter of 83–100 μ; its cells, numbering from fifteen to eighteen, measure 16·5 μ in diameter, and have no intercellular spaces. The procambial ring, 116·5–127 μ broad, consists of cells varying from 8·3–16·5 μ in diameter, the smallest being those on the cortical side.

The lignified elements are arranged in three xylem arcs, each of which consists of one or two small vessels 8·3 μ in diameter, and one large one, 16·5 μ in diameter, developed centripetally to the former. These vessels lie on the cortical side of the procambium, lignification not yet having proceeded internally towards the pith. The three alternating phloem masses consist each of three or four cells 5–6·5 μ in diameter. These have large nuclei, and even at this early stage an occasional fibre may be seen lying towards their external face.

The surrounding cortex is from ten to twelve cells broad, and intercellular spaces are present.

The stelar tissues are delimited by a single layered pericycle, and outside this is an endodermis with Casparian dots on the radial walls.

The piliferous layer does not produce root hairs till after the stelar system has become established: in several actively growing roots no hairs were produced for a distance of 4 cm. behind the apex, whereas xylem differentiation can be seen after a distance of just over 5 cm. The distance behind the apex at which root-hair production commences varies with environmental conditions, but in each case examined root-hair production was preceded by stelar elaboration. In the region where root-hair production is active, a sudden increase in the diameter of the root takes place: for example, an increase from 1000 to 1240 μ has been noted. This increase is due to both cell division and to dilatation of the individual cells. Thus the pith now measures 115×130 μ; its cells, numbering about thirty, vary from $16{\cdot}5–23 \times 26{\cdot}5$ μ in diameter.

No intercellular spaces have yet been formed. The breadth of the procambial ring remains the same, but the central cylinder has increased—an increase due to the pith. To maintain its continuity round that tissue, the procambium must have increased radially. The cortex has now a breadth of 465 μ, is ten to fourteen cells broad, these measuring from 33–66·5 μ in diameter. Increase in diameter of the root must be attributed mainly to activity in the pith. If the ratio central cylinder/total diameter be compared between this region of the root and the hairless region between it and the apex, it is found to be 1/5·4 and 1/4·7 respectively; if, however, the ratio pith/central cylinder be compared for the same regions, it is seen to be 1/1·9 and 1/2·33, *i.e.* an increase in the diameter of the root is accompanied by a decrease in the relative diametric proportion of central cylinder to pith, or the pith is expanding radially more quickly than the central cylinder. That this property of the pith has a marked effect upon the internal organisation of the root will be shown later on: while the value to the plant of the rapid increase in total diameter may be, as Jost (6) pointed out, that a certain tenseness is given to the root (thus rendering it more stable in the soil) when increase in thickness occurs after a period of rapid elongation. Jost also correlated this phenomenon with a concurrent decrease in length. No attempt was made

to discover if a decrease in length took place in the *Acanthus* root in this region, but the tendency for the cortical cells, especially the peripheral ones, to become elongated radially, in contradistinction to the tangential elongation as noticed in the region between this and the apex, suggests that a slight contraction in longitudinal dimensions may have taken place.

Maturation of stelar tissue continues by the addition of phloem cells on the tangential sides of the first formed ones and by addition of more lignified elements to each xylem ray. The elements added at this stage are intermediate in size between the two sizes of existing vessels, and are deposited centripetally and tangentially to the last-formed large vessels, the latter becoming enclosed in a circle of elements of narrower lumina.

Towards the proximal end of this region of root-hair production, a cambium arises in the outermost cortical layers, beneath the piliferous layer. This latter, by the dilatation of the root, becomes sloughed off, but is replaced by this secondary cambial activity, providing the root with a persistent piliferous layer, and hence persistent root hairs.

Persistent root hairs have been described in members of the *Compositae*, *Primulaceae*, and *Leguminosae*, and Whitaker (12) has shown that their presence is correlated with the lack of secondary thickening characteristic of the herbaceous type of root.

The case for *Acanthus* agrees with this statement. The cortex remains throughout the life of the root, becoming a storage tissue: its preservation is ensured by the lack of increase of the vascular cylinder, as will be shown, and by the non-development of a pericyclic phellogen. Whitaker found in the genera he studied that the development of these hairs occurred either at the proximal end of the root or at the distal. This is not the case in the *Acanthus*. Here the root hairs are developed from the distal to the proximal end; on any particular root or part of a root they may be seen either as a continuous covering or an interrupted one. On thick old roots, or on the proximal thicker parts of young roots, they are usually continuous, while on the younger more actively growing part of the root they tend to be discontinuous. Their disposition is given below on two roots, one 28 cm., the other 3 cm. long.

TABLE I.

DISTRIBUTION OF ROOT HAIRS.

Root 28 cm. long.

From tip backwards to	3·8 cm.	no hairs.
.. 3·8 cm. backwards to	15·3 ,,	hairs.
.. 15·3 ,, ,,	,, 16·8 ,,	no hairs.
.. 16·8 ,, ,,	,, 28 ,,	hairs and branch roots.

Root 3 cm. long.

From tip backwards to	7 mm.	no hairs.
.. 7 mm. backwards to	17 ,,	hairs.
.. 17 ,, ,,	,, 30 ,,	no hairs.

It is an accepted fact that root-hair production occurs behind the rapidly elongating region of the root apex, and Snow (8) has shown that root-hair production is correlated, not with the rate of growth of the organ, but with differential elongation of outer and inner tissues, being dependent on the ratio between "the capacity of the epidermal cells to elongate and their ability to do so." Thus, an epidermis tending to elongate more quickly than it is able to do so because of the slower elongation of the internal tissues throws its outer free walls into bulges, which extend into root hairs. In other words, when internal and external tissues are elongating equally, no hairs are produced: when the internal tissues are elongating more slowly than the external, root-hair production commences. In the young *Acanthus* root, then, the phenomenon of alternating hairless with hairy regions suggests alternating periods of rapid elongation of all tissues followed by periods of slower and differential growth, the slowest growth being in the central tissues.

The root-hair production started in the first region of differential growth behind the apex is continued backwards by means of the cortical cambium; hence it is natural to find that the hairless regions will show a decreasing length, passing from the apex backwards, till on the older parts of the roots the hairy covering is continuous.

Further, if the hairless regions are those of rapid and the hairy regions those of slower elongation, it might be expected that the latter would show an increased radial growth when compared with the former. This is usually found to be the case if the regions immediately behind the apex are considered. It has been said that in passing from the region

behind the apex to the region where root-hair production commenced, that an increase in diameter in one particular root took place from 1000–1240 μ; passing further backwards now into the next hairless region a decrease to 1150 μ was observed.

This difference is exaggerated in roots plunged straight into alcohol, in which medium the tissues in the hairless regions assume a shrunken appearance, especially in the cortex where the cells, mostly of the periphery, become elongated radially. The tissues in the root-hair region remain comparatively turgid. On account of this fact, measurements were made from hand sections of fresh material cut in water.

Despite the fact that the root has shown a decrease in diameter, cellular division in the pith has resulted in an increase, though slight, in that tissue. Cell increase has taken place from thirty to fifty, but no increase in the size of the cells has occurred; the presence of nuclei in some shows that this tissue is still in a state of activity.

The relative proportions of the tissues in the three regions just considered can be tabulated as under. (It will be seen that the tissue measurements which have been given are those of the diameters. From the physiological point of view, however, measurements giving the surface of contact between the various tissues would have been of more value, *i.e.* where actual size of tissue is considered, the area rather than the diameter is of more importance. When, however, the figures are used for comparative purposes, such as in the table below, where they are stated as ratios, the final result is independent of the actual measurements.)

Table II.

Comparative Dimensions of Tissues in Young Part of Root.

	Ratio: Central Cylinder/ Total Diameter.	Ratio: Pith/ Central Cylinder.
Region before root-hair production	1/4·7	1/2·33
Region of root-hair production	1/5·4	1/1·9
Region behind root-hair production	1/4·2	1/1·9

Thus between the last two regions a decrease in the proportion of central cylinder to total diameter has been effected concurrently with the maintenance of the relative proportions of pith to central cylinder, indicating a lag in radial expansion of cortical and procambial tissues proportional to pith. The effect of this will be discussed later on.

From this region backwards secondary roots are produced and in the procambial ring a fourth xylem arc has made its appearance. This arc is first seen by the appearance of a vessel of larger size—25 μ in diameter, round which smaller ones, 13 μ in diameter, are deposited. A regular feature of the development of the *Acanthus* root is the increase in the number of xylem arcs in transverse sections taken from the apex backwards, a feature which will be discussed later. In the formation of these arcs, the first-formed small elements characteristic of the first three tracts may be either absent or present.

Further increase in the lignified tissue of each ray takes place in a characteristic manner. Maturation of narrow elements, which, as was seen, were deposited round the large ones, continues in a centripetal direction towards the pith. At the same time, however, deposition of large vessels, measuring from 25×33 μ to 30×33 μ, occurs tangentially to the first-formed centripetally developed group, and their order of deposition is centrifugal. These latter are the second xylem elements of the primary wood, or the metaxylem of van Tieghem (10), who described them as arising in precisely the same manner in many species. In *Acanthus* no centripetal deposition of metaxylem relative to protoxylem occurs. The first group of elements are all protoxylem, and the metaxylem is tangentially disposed and centrifugally developed relative to them. This phenomenon, contrary to the usual centripetal deposition of metaxylem relative to protoxylem in many roots, results in the preservation of the pith as a parenchymatous tissue, which eventually becomes a storage organ. The xylem arcs at this stage present the appearance of an inverted "T," and consist of large vessels embedded in a mesh of narrow ones. As lignification continues, the deposition of metaxylem, while losing some of its regularity, extends towards the pericycle as two arms on either side of the protoxylem, and always is composed of large and small elements,

while towards the pith small elements only are matured. The net result of this process is a greater increase of each ray tangentially than radially.

Passing backwards into the next region of root hairs, diametric increase to 1665 μ has taken place, an increase again which must be attributed mainly to the central cylinder. This has now a diameter of 616·5–665 μ (compared with 265–280 μ in the previously described region); and again the seat of dilatation has been the pith, which has increased from 130–150 μ to 465–475 μ. This tissue has now a diameter of fourteen cells, these measuring from 25–66·5 μ (compared with 16·5–28 μ previously). The cortex shows an increase in breadth from 460–560 μ, due mainly to dilatation of the cells.

Increase in the number of xylem rays continues by the addition of one arc at a time, so that towards the distal end of a root a number varying from ten to thirteen has been observed. Tangential growth of each arc continues as described so that eventually, when they become united, the path is circumscribed by a complete lignified cylinder.

A transverse section through the root in the region having seven xylem arcs showed the following features: The pith has increased to a diameter of 600–665 μ; its largest cells, in the centre, measure 83 μ, while those round the periphery measure 25 μ. It is not easy to determine whether these peripheral cells are really pith cells. As has been seen, the root up to this stage has shown continued radial growth by cellular activity of its own tissue. The indications now are, however, that increase in diameter is due to the innermost procambial cells, which only giving rise to narrow lignified elements on the xylem side, are maturing into pith cells on the interior.

The xylem rays have not yet united, and have radial and tangential dimensions varying from 58–66·5 μ and 130–200 μ respectively.

Between these xylem rays and the alternating phloem a well-defined and almost continuous cambium is differentiated. A noteworthy point is that between the xylem rays the procambium, due to stretching over a dilating pith, is much narrower, so that here the cambium almost abuts on the pith. Union of the rays is effected a little farther back

by the lignification, on the periphery of the pith, of a narrow strip of small elements only, across these remaining portions of the procambium. The xylem arcs are not usually disposed at equal intervals round the pith, so that some of the last portions to lignify are longer than others. A transverse section through the regions in which the xylem ring was almost complete showed one lignified portion 130 μ long. The xylem varied in breadth from 16·3 μ (on the side of a ray where it consisted of one element only) to 130 μ in the primary ray.

The stele now assumes an aspect differing from previously described regions. The xylem cylinder, when complete, is cylindrical on the pith side, but on its outer face consists of a series of ridges and furrows due to continual deposition of both wide and narrow elements opposite the primary rays, but narrow elements in the interfascicular regions. The irregularity of the outer face causes the outline of the cambium, which follows the outline of the xylem, to be sinuous. With the completion of the xylem ring, and the ensuing commencement of cambial activity, the root has completed its primary growth; the most outstanding features of this have been the continual dilatation of the pith and the increase in the number of root poles. Secondary increase due to the cambium follows immediately on completion of primary growth, and as secondary and primary tissues are histologically similar (with the exception of the protoxylem) no difference can be detected between the two.

From the time of completion of the vascular ring, and just before this event, onwards, differences in development occur, these differences being correlated with the behaviour of the pith relative to the xylem cylinder.

Two sets of conditions arise—

(1) In which dilatation of the pith ceases before, or when, the cylinder is complete.

(2) In which the cylinder is complete before dilatation of the pith has ceased.

(1) If in a root in which the lignified cylinder has become complete the pith is mature and has ceased to dilate (a condition usually attained when about fourteen cells in diameter and measuring 665 μ), further development consists simply in the maturation of vascular tissue, from procambium at

first, and then from cambium, in the normal way. The pith when mature has intercellular spaces and its cells are packed with starch grains as also is the cortex, but here the intercellular spaces are larger. The outermost cortical layer continues to be meristematic, producing a piliferous layer externally and cortical tissue internally. The peripheral cortical tissue is thus secondary, but no sharp distinction is seen between primary and secondary regions; the only distinguishing features of the latter tissue being the smaller size of the cells, their tendency to tangential elongation, and the less frequent occurrence of intercellular spaces.

Secondary xylem formation of the normal type is very scanty, and as no internal phellogen arises to cut off a cork layer the cortex never becomes exfoliated, but remains as a storage organ for starch. In old woody roots the demand for an increase in conducting tissue is satisfied by development of lignified tissue in the pith. It has not been observed whether this is due to activity of an intrastelar cambium arising later in development in that tissue (except in the special case to be considered shortly), or whether it is due simply to maturation of the pith cells themselves into vessels. Development of this tissue takes place from the periphery of the pith inwards, which tissue may become either partially or completely transformed. Histologically this lignified tissue is similar to that of the vascular ring, but no phloem has ever been observed.

(2) The case is quite otherwise, however, if the lignified cylinder is complete, or almost complete, before the pith has stopped increasing in diameter. The latter exerts a distending force on the former, which, being rigid and incapable of stretching, ruptures. The rupture occurs first, at any rate, in one of the least lignified interfascicular regions, but as dilatation of the pith continues, complete fragmentation of the stele ensues; the isolated fragments corresponding to the primary rays.

Thus a root which before the xylem ring became continuous had a pith measuring $300 \times 500\ \mu$ in diameter, and one unlignified interfascicular strip of procambium $130\ \mu$ long had, when the pith had increased to $330 \times 580\ \mu$, an unlignified strip $250\ \mu$ long. In the region behind this, the pith had increased to $465 \times 665\ \mu$, the unlignified ray had become

330 μ long, while other gaps of 50–80 μ had occurred between the primary rays. Reunion of the xylem rays across these gaps takes place by cambial activity, when dilatation of the pith ceases. Before this, however, other changes have occurred. Ensuing on its tendency to follow the outline of the xylem, the cambium has penetrated into the bottom of the furrows on the external face of the cylinder, and when

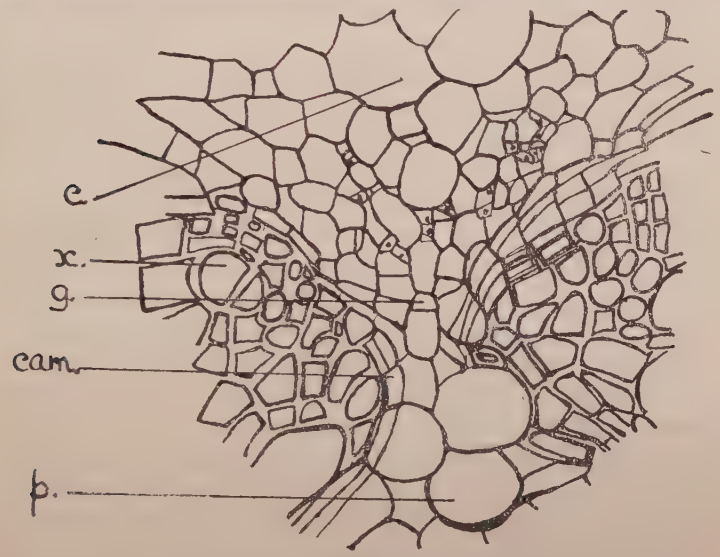

FIG. 1.—Rupture of cambium and intrusion into pith.
c=cortex; *p*=pith; *g*=gap in xylem; *cam*=cambium intruding into pith; *x*=xylem.

rupture of the lignified ring has taken place in these furrows the cambium likewise becomes broken. The fractured ends of the cambium now continue their way round the sides of the xylem fragments and enter the pith round the periphery of which tissue they penetrate to various degrees (fig. 1). In some cases they join up to form an almost continuous ring. Reunion of the extraxylary cambium is effected on cessation of pith dilatation by certain cells in the path of the original cambium becoming meristematic and restoring the continuity of that tissue, and this then proceeds to mature the xylem closing the gaps. The intraxylary cambium differentiates lignified tissue round the periphery of the pith.

Anomalies in the vascular system of the Acanthaceae have

been described by Hérail (5), who confined his attention, however, to the stem. In *Hexacentris* and *Mendonica* irregular deposition of large and small lignified elements on the outside of the stele gives the latter a furrowed outline, as described here in the root of *Acanthus*. In these genera, however, secondary xylem formation is more active, and the rapidly increasing ridges finally rupture the cambium across the furrows; union is effected later by the fractured ends of the cambium growing together as observed in *Acanthus*. From Hérail's work it is obvious, then, that the irregularity in the outline of the xylem is in itself, provided it becomes sufficiently pronounced, enough to cause discontinuity of the cambial ring.

In the *Acanthus* root under consideration, however, there is the extra contributory cause, namely, the dilatation of the pith, probably a much more disturbing factor than xylem irregularity.

The disintegrating effect on the stele of a distending pith has been shown in some of the lower plants. Wardlaw (11) has shown that in the stems of *Psilotum*, *Tmesipteris*, and *Lycopodium* passage from a young stem to an old one is accompanied by "progressive decentralisation and disintegration of the xylem." These phenomena he interprets on Bowers's Size Factor theory, the structural changes being effected to maintain a high proportion of surface to bulk in the xylem tract.

Such an interpretation may be used to explain the development of the primary state common to all *Acanthus* roots—the concurrent dilatation of the pith, decentralisation of the stele, and increase in the number of xylem tracts being expressions of the same underlying principle. The fact still remains to be accounted for, however, that fragmentation of the xylem occurs only in some roots and not in others. It is a significant fact that the anomaly, where it occurs, is due to dilatation of the pith after the establishment of the xylem ring, whereas in the other case continuity of the xylem is preceded by maturity of the pith. The controlling factors, then, must be those either delaying pith development relative to xylem formation, or causing it to develop after it normally would have stopped.

The explanation is found by comparing the origins of

these roots. The plants used for this investigation were all raised from stem cuttings of various ages. Some consisted of young pieces of stem in which the vascular system consisted of discrete vascular strands, and in which tissue differentiation was still proceeding; others were older stems in which the conducting tract had become a complete ring. From the latter the normal type of root was produced, while roots showing the anomalous structure were derived only from young stems.

Further, the anomaly has only been observed at the proximal end of such roots, just outside the point of emergence from the parent organ. In the case of a root arising from a stem where primary tissue is mature, the base of the root is in continuity with tissue which has ceased to dilate, and therefore can have no distending influence on the basal root regions. In the case of a root, however, arising from a stem still undergoing primary tissue dilatation, the tissue of the stem abutting on the root base, if increase takes place, will have a distending effect on the basal root tissues. This effect is all the more pronounced if the root arises from the stem while still in the discrete vascular strand stage. The root, arising in the proximity of one of the strands or between two strands, has a base broad enough to abut on the interfascicular meristematic tissue. This tissue, actively dividing, considerably disintegrates the stelar system of the young root inside the stem, and this activity progressing a little way down the root gives rise to phenomena just described. In fact, in roots produced from the first or second nodes or internodes the stelar system of the root at its extreme proximal end often consists of a number of quite isolated xylem strands, each completely surrounded by a cambium.

Fig. 2 (ii–v) shows the proximal end of a root produced from a cutting made through the first node. Here the arc-shaped portion of xylem is derived from the primary ray of the stem, while the isolated strand (*acc. st*[*r.*]) is derived from one of the accessory leaf traces, the cuttings having been made just above the point of union of this strand with the central cylinder of the stem.

It is thus seen that the degree of stelar complexity of the parent organ exerts an influence on the internal construction of the adventitious root produced from it, at least at its point

of insertion, this influence depending upon whether or not the tissue of the young root is in connection with dilating tissue of the stem.

The Branch Root.—The branch root is somewhat slender, and is characterised in the majority of cases by a diarch stele.

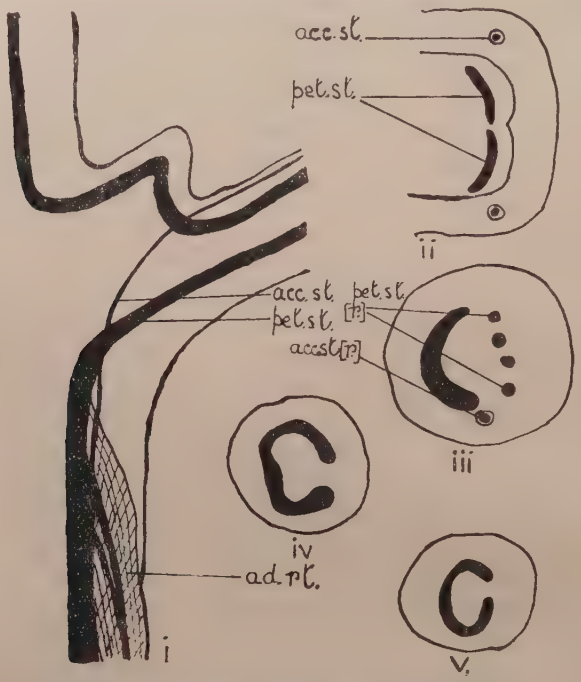

FIG. 2.—Development of root from a nodal cutting.

i. L.S. through half of the node, showing the base of the root which has arisen from the main petiolar strand. ii–v. T.S.'s through stem and root. ii. Stem above region of root junction. iii. Root at junction with stem. iv and v. Root below junction.

pet. st. = main strand of petiole; *pet. st*[*r.*] = root strand connected with above; *acc. st.* = accessory strand; *acc. st*[*r.*] = root strand connected with above; *ad. rt.* = junction of adventitious root and stem.

The pith is small, and becomes completely lignified at a much earlier stage of development than in the parent root. No fragmentation of the xylem cylinder has ever been noticed in the branch root, and pith dilatation only occurs to a slight extent.

Ontogeny of the Aerial Root.—A point of considerable interest in the ontogeny of the soil root of *Acanthus* is the increasing

number of xylem arcs passing from the apex backwards. Before this question is discussed, however, it is necessary to follow the development of the aerial root.

The aerial root is initiated in the pericycle as is the soil root, and emerges with an internal organisation similar to the latter. The growing point is broad, but soon differs from the soil root in that as it enters the atmosphere it becomes broader and bulkier in contradistinction to the thinning of the root after entering the soil. The reason for this becomes obvious if a series of transverse sections behind the tip be examined. Immediately behind the apex the three histogenetic regions are well defined, but their relative proportions differ from those of the soil root, the outstanding difference being narrowness of the cortex and the breadth of the central cylinder compared with that of the soil root. The following figures show a comparison between the two types of roots :—

TABLE III.

	Soil Root.	Aerial Root.
Total diameter . .	1500 μ	1500 μ
Cortex	460 μ	250 μ
Central cylinder . .	580 μ	1000 μ
Pith	470 μ	500 μ

The most distinctive feature as shown by these figures, then, is the rapid increase in breadth of the procambium, at the expense of the cortex. This region is immediately behind the root cap; the next stage in development, following closely on the above, is the rapid increase in breadth of the cortex. Thus in the above root the cortex attained a breadth of 415·5 μ while the central cylinder was still 1000 μ in diameter. To this rapid increase in breadth, of first the central cylinder and then the cortex, is attributed the bluntness of the growing point of the aerial root.

A very important difference between the two types of roots is the large diameter attained by the central cylinder of the aerial root immediately behind the apex, largely due to procambial dilatation, compared with that of the soil root.

In fact, in the former the procambium attains almost its

mature dimensions before the stelar elaboration commences, whereas, as has been shown, the soil root shows progressive increase of procambium from the apex backwards. Correlated with this type of growth, the aerial root elongates very slowly, a fact which suggests that in air the histogenetic tissues in the apex are increasing radially much more actively than longitudinally, whereas in the soil the reverse is the case.

Resulting from this difference between the two types of root apex are differences in the anatomical features of the mature tissues. In the aerial root the pith and the procambial ring attain their full size, or almost so, before differentiation of phloem and xylem commences. Before lignification begins the procambium is ridged and furrowed, the number of ridges being usually about ten. In the ridges the primary xylem groups are found, by the differentiation in each of from one to three rows of narrow elements, matured centripetally.

The development of the xylem cylinder proceeds as in the soil root, elements being matured tangentially and centripetally, the latter, however, only to a limited extent: the greater tangential deposition of elements soon leads to the lateral union of the primary rays forming a continuous ring round the pith. No increase in the number of primary rays takes place in the aerial root, as all the rays are matured at the same time behind the apex.

The xylem ring differs histologically from that of the soil root in the small number of narrow vessels formed compared with the large amount of narrow elements.

The large metaxylem vessels are disposed much more regularly on the sides of the protoxylem than in the soil root. On completion of the ring the cambium becomes continuous and proceeds immediately to differentiate secondary tissue. Large vessels are deposited mainly in lines continuous with the metaxylem, the rest of the tissue consisting of narrow elements. Primary rays of parenchyma are usually formed between the primary xylem rays; and after secondary growth, secondary rays commence opposite the protoxylem.

All secondary formation of conducting tissue in the aerial root is normal on the outside of the primary body, no conducting tissue being formed in the pith. Secondary increase is much more pronounced than in the soil root, producing a wide xylem cylinder. The cortex is never exfoliated.

Consideration must now be given to the nature of the covering of the root. Behind the apex, while primary tissue growth is proceeding, a cambium on the outside of the cortex cuts off a layer of suberised tissue. This provides the root with a protective layer for some distance backwards, but later, notably after the completion of the xylem ring, this cambium produces a dense mass of hairs. These persist from this stage onwards back to the proximal part of the root, and may be replaced again by a cork layer only in old and very woody roots after considerable secondary increase has taken place and the cortex itself has become impregnated with fatty substances.

These hairs are unicellular and resemble the root hairs of the soil root, and are produced so thickly as to provide the root with a thick felt-like covering.

The presence of starch grains is only noticed in old woody roots, when they are present in both pith and cortex.

The main features distinguishing the aerial root from the soil root, then, are (1) its much broader growing point, (2) differentiation of the primary xylem body round a mature pith, (3) secondary increase of conducting tissue on the outside only of the primary, (4) retention of the pith (which is larger relative to cortex than in soil root).

The aerial root of *Acanthus* on entering the soil shows a change in internal construction corresponding to the change in environment. This consists in the reduction of the breadth of the growing point and the ensuing assumption of the characters of the soil root—decrease in size of pith and contraction of the stele into a more central position and lack of secondary tissue formation external to the primary. The change takes place gradually, a series of transverse sections above and below soil level showing just a gradual decrease in the diameter of the pith, concurrent with an increase in the amount of large vessels and decrease in small ones.

Comparative Anatomy of Soil Root and Aerial Root, and its Bearing on Ontogeny.

It has been shown that the soil root differs ontogenetically from the aerial root in the gradual increase in the number of root poles passing from the growing apex backwards, or, in other words, the reduction in the number of these in the

younger parts compared to the older. Reduction phenomena in the number of root poles in the radicle have been pointed out by Dodel (3), who showed that in *Phaseolus* that organ possessed more xylem tracts towards its proximal than at its distal end. These extra strands he showed were accessory cotyledonary traces, alternating with the usual root poles; they differ from the strands in *Acanthus*, however, in that they only pursue a short downward course into the root before terminating, either singly, or after uniting in pairs. Bond (2) describes similar phenomena in *Vicia* as well as in *Phaseolus*. The results of both of these authors show that in these species examined a correlation exists between the presence of a pith and the number of xylem strands. Thus in the radicles of these species a pith exists in the proximal region of the root where it merges into hypocotyl, but disappears towards the distal region. Here a central xylem core is formed, consisting of fewer arcs than in the conducting system differentiated round the pith at the proximal end. Bond furthermore found that decotylation led to the slower growth of the radicle, with the ensuing attention of the pith and accessory strands for a longer period.

In the root system of the Corsican Pine, Aldrich-Blake (1) has shown that not only root-pole reduction, but the reverse process of augmentation may take place, the latter process accompanying an increase in diameter of the root. In view of the above considerations, then, it is not unnatural to expect that in the root of *Acanthus* the number of arcs should show a correlation with the dimensions of the pith. The following table shows how reduction has occurred in a root 28 cm. long :—

TABLE IV.

XYLEM-ARC REDUCTION IN THE SOIL ROOT.

Distance behind Tip.	No. of Xylem Arcs.
8 mm.	3—the 4th just forming
4 cm.	4
8 „	4
12 „	5
16 „	6
20 „	6
24 „	8
26 „	9
28 „	10

Likewise, as has been shown previously, the pith shows a gradual diminution from the proximal to the distal end, and that there is a correlation between the two sets of phenomena can be seen if the relative dimensions of the tissues be compared. This is illustrated by the following figures :—

Table V.

Comparison between Stelar Structure and Tissue Dimensions in the Soil Root.

Degree of Stelar Differentiation.	Ratio: Diameter of Pith/ Diameter of Central Cylinder.	Ratio: Diameter of Central Cylinder/ Total Diameter of Root.
3 xylem arcs	1/2·33	1/4·7
4 ,, ,,	1/1·9	1/4·2
5 ,, ,,	1/1·4	1/2·6
7 ,, ,,	1/1·4	1/2·4

Thus increase in the number of arcs is accompanied by a decrease of central cylinder relative to pith, but an increase in central cylinder relative to total diameter. The actual increase in diameter of the central cylinder is clearly to be attributed mainly to the pith; hence the determining factor accompanying root-pole increase is the increase of pith relative to total diameter; in other words, when the pith has attained a given relative diameter, stelar complexity will have attained a correspondingly high degree.

Comparing now soil root and aerial root, it has been seen that in the former the complete primary stelar system is only established gradually over a considerable length of root, whereas in the aerial root the whole primary system is established at the same time, shortly behind the apex.

The following figures obtained in an aerial root may be contrasted with those in Table V :—

[Table VI.

TABLE VI.

COMPARISON BETWEEN STELAR STRUCTURE AND TISSUE DIMENSIONS IN THE AERIAL ROOT.

	Ratio: Diameter of Pith/ Diameter of Central Cylinder.	Ratio: Diameter of Central Cylinder/ Total Diameter. of Root.
Procambium just noticeable .	1/2	1/1·5
Histogenetic regions well defined	1/1·5	1/1·8
Before xylem formation . .	1/1·2	1/1·8
Xylem differentiation begun (19 arcs)	1/1·2	1/1·09
Tangential elongation of arcs	1/1·2	1/1·09
Secondary thickening commenced	1/1·4	1/1·06

(The last figures show that after commencement of secondary thickening the proportions are upset, and are therefore not valid for comparative purposes. It must therefore be emphasised that the phenomena under consideration are those of the primary root body only.)

The increase of the ratio central cylinder/total diameter from 1/1·5 to 1/1·8 and its subsequent decrease to 1/1·09 is due to the rapid dilatation of the cortex behind the tip, as previously described. Apart from this, however, the figures show that in the aerial root the final relative proportions of all tissues are attained much sooner behind the growing point than they are in the soil root; and consequent upon this precocious attainment of the mature size of the central cylinder is the formation *ab initio* of the total number of primary xylem arcs.

The question now arises, To what is this difference in organisation behind the growing point due?

On its initiation in the parent axis the aerial root and soil root have a precisely similar internal morphology; the subsequent difference in organisation must therefore occur after emergence into either soil or air.

Examination of a young soil root throws some light on this point, as is shown in the following table of figures obtained in a root 15 mm. long :—

TABLE VII.

COMPARISON BETWEEN STELAR STRUCTURE AND TISSUE DIMENSIONS IN A YOUNG SOIL ROOT.

Distance behind Tip.	Degree of Stelar Differentiation.	Ratio: Diameter of Pith/ Diameter of Central Cylinder.	Ratio: Diameter of Central Cylinder/ Total Diameter of Root.
5 mm.	No lignified elements	1/1·23	1/2·5
10 ,,	6 xylem arcs	1/1·3	1/2·5
15 ,,	10 ,, ,,	1/1·27	1/2·85.

These figures show that roughly the same proportions between pith and central cylinder have been attained (*cf.* previous tables) as in the older root and the aerial root when the vascular ring has the large number of xylem arcs.

Further, this ratio has been attained much sooner behind the apex in the young soil root than in the old, and hence approximates more nearly to the aerial root. From the latter it differs, however, in that root-pole reduction has begun. In other words, this young soil root resembles the aerial root in that the degree of stelar complexity is greater behind the growing point than in the older root, but as elongation has proceeded this degree has diminished, and its diminution is correlated with the relatively less proportional radial dilatation of central tissues to peripheral tissues.

Reference to Table VI again shows this point. In the proximal part of that root, *i.e.* the part of the root formed when young, a new xylem ray appears, each 2 cm., while in the distal region the root had elongated 11·2 cm. between the deposition of the fourth and fifth arcs, *i.e.* stelar elaboration has been a quicker process behind the apex of the root when it was young than when it has become older. Further, it is seen that between the appearance of the xylem arcs in the younger part of the root there has been much more rapid elongation than has occurred in the older parts when their tissue differentiation was proceeding. In this phenomena lies the clue to the problem. The young root after its emergence is dilating radially more rapidly proportional to longitudinal growth,

but after it has penetrated the soil for some distance, it elongates more rapidly with a consequent reduction of radial increase.

In the aerial root, on the other hand, the tissues dilate more quickly behind the growing point, with which is correlated the slow longitudinal growth of such an organ.

The facts, then, as understood so far for the development of the root, may be summarised as follows:—

(1) The root initial is the same in soil and aerial root: it is broad, and has high degree of stelar elaboration behind the apex.

(2) On entry into the soil, rapid longitudinal increase takes place with a concurrent diminution in radial increase and in stelar complexity.

(3) On entry into the atmosphere, slow longitudinal increase is accompanied by greater proportional dilatation of the tissues and the maintenance of a high degree of stelar complexity behind the apex.

(4) In all cases the degree of stelar elaboration is correlated with the relative proportion of central cylinder, especially pith, to total root diameter. The cortex remaining practically the same breadth after its embryonic state has been passed, differential growth between central tissues and cortical tissues is suggested. When the central tissues dilate more rapidly relatively to the cortex, a stele with a correspondingly large number of xylem arcs is formed; when dilatation of the central tissues is relatively slower than the cortex, only a few xylem arcs are formed.

The fact has been referred to previously that in the root of *Acanthus* the tissues at the extreme tip, under the root cap, do not show definite stratification into the three histogenetic regions until farther back; this confusion of tissues, according to Flahault (4) is due to the intensity and equality of cellular increase of all regions in this area, *i.e.* central cylinder and cortex are differentiating with equal regularity. It follows, then, that the width of central cylinder relative to cortex as initially laid down will be maintained as long as growth in this manner proceeds, and any condition altering the relative growth of the two tissue regions will be followed by the difference in stelar complexity already described.

Consider now the root entering the soil. A period of rapid

elongation ensues, followed, as has been shown when discussing root-hair production, by a period of slower elongation. The first phase, being devoid of root hairs, is indicative of equal longitudinal extension of all tissues; the second phase, where root-hair production commences, is due to differential growth between peripheral and central tissues.

Fundamentally the same process, therefore, appears to control both degree of stelar complexity and root-hair production. It was seen that the stele has its foundations laid down before root-hair production commences, *i.e.* while uniform elongation of all tissues is taking place behind the apex. With the slowing down of longitudinal increase in the region behind this, differential growth between central and peripheral tissues ensues, resulting in greater dilatation of the former tissues proportional to the latter, or, in other words, the slowing down of longitudinal increase is more marked centrally than peripherally. The result for the central tissues is increase in stelar elaboration, and for the peripheral tissues the production of root hairs.

Considering now the aerial root, slow growth in length maintains the equal longitudinal increase of all tissues. Hence for some distance backwards from the tip no root hairs are produced. Further back, however, root-hair production becomes intense, suggesting a greater tendency to elongation of the epidermal than the central tissues. This may possibly be due to the fact that in this case the epidermis becomes green and hence photosynthetic; the occasional starch grains seen in the green parts of the root have been suggested by Taylor (9) as being the transitory products of photosynthesis.

On the other hand, in this region xylem differentiation is proceeding much more rapidly than in the more distal region, and the effect of maturation of lignified tissue in itself might be a retarding one on the peripheral tissue.

Again, differential growth here might simply ensue on the slowing down of longitudinal increase, the central tissues slowing down more rapidly than the peripheral ones.

To conclude this discussion, then, it is seen that the determining factor on the ultimate construction of the primary body of the root is to be found in the nature of histogen differentiation behind the growing point. In the soil the plerome elongating more rapidly is contracted in breadth, and leads

to the centralisation of the stelar tissue; in the air it elongates slowly and becomes dilated, leading to stelar decentralisation. That this difference is due to the effect of environmental conditions on the growing apex is strongly suggested by the fact that the aerial root in penetrating the soil assumes corresponding internal features, but what the factors are which exert the determining influence it has not been possible at present to investigate.

Summary.

1. The root system of *Acanthus* consists of both aerial and soil roots.

2. The aerial root has an internal construction resembling that of a stem in the width of the pith and peripheral position of the conducting system, while the soil root has a centralised vascular system.

3. The aerial root on entering the soil shows corresponding anatomical changes.

4. The difference in construction between the two types of roots can be traced to the growing point, in which region it results from a differential growth between the histogenetic tissues, corresponding with the environmental conditions in which the root tip is growing.

5. The purely mechanical conception of the aerial root being produced as a "prop" is refuted; its production is to augment the deficient vascular supply of the stem.

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Propagation from the Leaf of Acanthus.

By A. McMartin, B.Sc., Ph.D.

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The anatomical changes involved in the production of adventitious organs by *Acanthus* when the stem, root, and leaf of that plant are used as cuttings have already been described by Taylor (2). A repetition of similar experiments yielded results which in the main agreed with those of Taylor as far as stem and root cuttings were concerned, but which differed fundamentally in the case of leaf cuttings. In view of this fact, and due to the interesting comparison which it has been found possible to make between the anatomical changes occurring in regeneration from the leaf and those in the hypocotyl of the seedling, the following account is given in much greater detail than by the previous author.

Anatomy of the Petiole.

The petiole of *Acanthus* in transverse section is cylindrical, with an average diameter of about 3 mm. The vascular system consists of one main central strand and two small accessory ones, situated in the cortex towards the adaxial side of the main strand.

The cortex is clearly demarcated into an inner region with large cells containing starch grains, and an outer region consisting of three to four rows of small collenchymatous cells.

The main strand of the vascular system leaves the stem as an arc, but after the departure of the bud trace the arc closes in so that the strand becomes cylindrical. The pith is small, $250 \times 330\ \mu$; in the centre the cells are thin-walled; round the periphery they are smaller and collenchymatous. Starch is stored in the pith.

The xylem is in a continuous ring, consisting of vessels and parenchyma cells. No cambium is normally present. Phloem is present to a considerable extent, and is surrounded by a pericycle one or two cells broad, and a well-marked starch

sheath. Pericyclic and phloem fibres are few, or absent altogether.

The accessory strands each consist of a central core of from four to six xylem elements, surrounded by phloem and a single-layered pericycle, in which a few fibres are sometimes present. No starch sheath has been observed.

Regeneration from the Leaf.

Isolated leaves grown in a propagating case maintained by bottom heat at a temperature of from 75°–80° F. after a week regenerate a root system from the cut end of the petiole. The roots are initiated in the vascular system, of which the main strand may produce one large one, or two small ones, and each accessory strand may produce one. Thus from one to four roots may be formed. After it has produced a branch-root system a swelling appears on one side at the top of each root, just below its point of emergence from the petiole. This swelling increases in size and soon gives rise to one or more small buds. Usually only one develops into a shoot, or if more than one develops one is much stronger than the other, or others. The shoot, after it has a few leaves expanded, generally produces an adventitious root of its own. After this an abscission layer forms across the base of the petiole, and the leaf withers away. A leaf-cutting one year old shows the remains of the petiole attached to the individual to which it gave rise. Even after the shoot has been produced the swelling from which it arose may continue growth, attaining in some cases the size of a pea. The other buds may be induced into growth by removal of this shoot, and an interesting feature is the haphazard manner in which the buds are formed over the surface. No polarity such as is characteristic of root or shoot appears in this organ.

The first leaves produced on the shoot show juvenile characters. If propagation be now effected from one of these juvenile forms, the leaves produced in turn from the new shoot show still further development of juvenile characters, notably in a great reduction in size and in simplicity of outline. In this way, after two generations of cuttings, a leaf was produced which was barely one inch long when full grown and had an entirely simple outline except for a notch at the apex.

The leaf of *Acanthus* shows remarkable plasticity in its regenerative powers. Thus a leaf severed in two by a cut at right angles to the midrib through the centre of the leaf will produce adventitious roots from the base of the midrib in each half; or if the leaf be split longitudinally down through the centre of the midrib and petiole, and each half planted horizontally, adventitious roots are produced in two or three places along the midrib, as well as from the end of the petiole.

Attempts to regenerate new growths from the isolated petiole have met with repeated failure. The same fate attended attempts to produce buds on the petiole after the root system was established. This was done by planting the leaf, and then, after the roots were produced, removing the blade, leaving only the petiole with roots attached. In most cases, however, all growth stopped; or if growth did proceed long enough, in which case it was very slow, for bud production, the buds were found in the normal manner at the top of the root. In no case did they make any further growth, however, after their appearance.

Initiation of the Root.

The root arises in the pericycle a little way up from the cut end of the petiole, and grows downward and out through the base. The young root is usually of such a size that its base covers half of the vascular ring of the petiole strand. Activity is not confined, however, to the arc which gives rise to root but extends round the pericycle on either side.

Moreover, activity is not confined to the pericycle. From this region it spreads inwards into the phloem and parenchyma of the xylem ring. This tissue, which is simply the unlignified part of the procambium, divides rapidly and in many cases displaces some of the xylem elements laterally and radially. A cambium now makes its appearance, being more pronounced in the region of the petiole immediately above that in which the root is produced. This cambium proceeds to form new xylem elements which considerably increase the breadth of the xylem ring, and, differentiating downwards, enter into the root. In one case an increase in breadth from 185 μ to 450–500 μ was noted.

Activity of the pith has caused a slight dilatation of that tissue

radially, resulting in a distension of the vascular ring, which also by the activity of its parenchyma has lost its compactness at the base of the petiole.

The root from the accessory strand is likewise pericyclic in origin.

Formation of the Swelling.

A root borne on a petiole has, when about one inch long, the same external appearance as a stem-borne root in that no sign of any swelling can be seen. A series of transverse sections cut from the tip upwards shows the same sequence of events as in the normal root, until the region just below the petiolar base is reached. The three xylem strands at the distal end (fig. 1) become augmented as the root increases in diameter towards the proximal end, and the construction of the stele corresponds in every way with a stem-borne root, with the exception that the alteration in outline from cylindrical to arc-shaped becomes accentuated by the greater increase in breadth of one of the interfascicular portions of the ring and the indentation and activity of the cambium. This is shown in fig. 1.

Concurrently with this, the stele becomes compressed on two sides, resulting in the reduction of the pith to a strip of tissue only one or two cells broad (fig. 1), with on one side a row of three or four xylem strands and on the other a delimiting tissue consisting only of endodermis, pericycle, and cambium, with a xylem strand only at each end.

Above this region signs of activity are seen in the stelar tissues, especially at one of the narrower ends; at this point (fig. 1, *p.*) slight dilatation of the pith has occurred, a condition which has been accompanied by activity in the cambium which has become more pronounced round that end. Higher still, changes have occurred which have no parallel in the development of the stem-borne root. The cambium activated at the dilated end of the stele has ruptured between the two xylem strands, and the broken ends, growing out almost at right angles to their previous path, have entered the cortex.

The penetration of the cortex by the cambium extends almost to the periphery, and the cortical tissue between the two strands becomes densely protoplasmic and shows signs

of cell division. This is more pronounced in a group of cells towards the periphery which foreshadows the bud.

The region above this shows a still more advanced stage of cortical activity in that a sheet of meristematic tissue, roughly

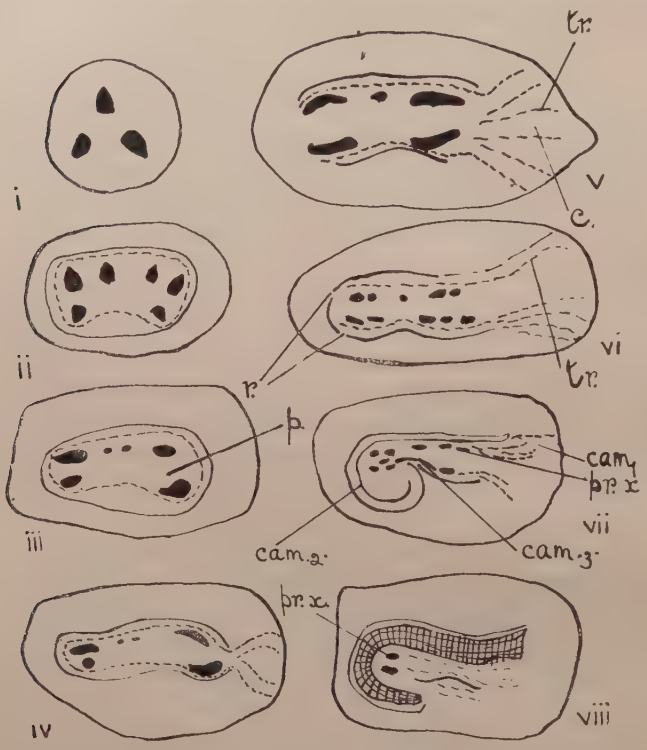

Fig. 1.—Changes leading to formation of swelling on top of root.

p. = dilating region of pith; *c.* = meristematic region in cortex; *r.* = ruptures in cambium; *pr. x.* = primary xylem; *tr.* = tracheids; *cam.* 1, *cam.* 2, *cam.* 3 = cambium.

i. Behind root tip. ii and iii. Compression of stele to form an arc, and dilatation of pith. iv and v. Rupture of cambium and penetration of latter into cortex. vi, vii, and viii. Destruction of primary vascular system and formation of secondary.

triangular (fig. 1, *c.*) extends from the stele outwards. In this tissue the identity of the cambium as such has practically disappeared, the whole region having a more or less uniform appearance. Close examination, however, reveals the existence of a few tracheids in paths corresponding to those in which the cambium would lie (fig. 1, *tr.*). Further, the densely

protoplasmic area noted previously is more pronounced, both in density and extent, and activity in the pith with its distending effect on the stelar system has caused a rupture of the cambium at one or two points between some of the xylem strands (fig. 1, *r.*), the cambium in the indented point of the ring, however, remaining complete. The cambium itself is in an active state of division, a condition more marked in the fragments on the outside of the arc than in the unbroken part opposite. Passing higher, cambial activity has increased especially at the narrow end of the stele opposite to that in which it was noted lower down the root. At this end a rupture has been effected, but no intrusion of the cortex has taken place: cell division of the cambium here takes place *in situ*, and merely increases the width of the tissue. Also, activity of the pith has resulted in the displacement of the primary xylem rays, which have become dispersed merely as scattered lignified elements (fig. 1, *pr.x.*).

The final disintegration of the primary structure occurs immediately above, at the base of the root. Here the vascular cambium has united along the outside of the arc, and has curved round that narrow end of the pith where activity was noted to be most intense (fig. 1). Activity at the opposite end, *i.e.* where lower down the cambium intruded into the cortex, has not had the same result here, the whole of the cambium functioning in the formation of secondary stelar tissue. The remaining tissues, cortex, and pith, are also in a state of activity, especially the latter.

The outline of the stele at this stage is characterised by its incompleteness, and due to its formation from the cambium from the outside of the arc, and round one end only, it is hook-shaped (fig. 1). It is worthy of note that the missing part of the system is on that side from which lower down the cambium invaded the cortex. Also, the stelar tissue is entirely secondary, the primary body being in a state of complete disintegration and consisting only of a few scattered elements (fig. 1, *pr.x.*) which lie across the pith obliquely, facing across or towards the gap in the secondary body.

Leaving now the root, transverse sections through the base of the petiole show that the vascular system here is dual in origin, in that the xylem being matured from the petiolar cambium is differentiating downwards round the true root

system. Moreover, the secondary tissue of the root is in continuity with this secondary petiolar tissue, and a gap which has been formed at the base of the petiole strand, due to dilatation of the pith, is in continuity with the gap in the secondary root tissue.

It will be clear, then, that the arc-shaped outline of the root stele towards its proximal end is due to its mode of union with the petiolar conducting system, especially if it is borne in mind that originally only an arc of the continuous ring of the main strand took part in the elaboration of new tissue.

These series of changes have been described as taking place from the distal to the proximal end of the root, but, obviously, the order in which they would take place in the plant would be in the reverse direction, secondary changes proceeding from the older to the younger parts. By considering them in the manner just adopted, however, a reconstructed account is made possible of the sequence of events in each particular region, as *within limits* the stage at present reached by the more distal parts will reflect to some extent the order of development of the more proximal.

Considering now the changes that have occurred as a whole, the most salient features are (1) the beginning of secondary changes in the conducting system at a time when in normal root development the primary body is not complete. This series of changes have as their necessary precursor the premature activity of the vascular cambium, and (2) the destruction of the primary body by dilatation of the pith.

The fact must be taken into account here that the region under consideration is at the junction of petiole and root, a region where the materials drifting downwards from the leaf will meet the upwardly moving solutes from the root. An accumulation of material will follow, which having no outlet will be productive of peculiar physiological conditions with accompanying abnormal anatomical requirements, principal among which will be a gradually increasing pressure on the surrounding tissues and the demand for an augmented conducting system. Now, it was seen that the earlier changes which occurred were increased activity in the pith and the commencement of activity of the vascular cambium; the former, ultimately resulting in the complete disintegration of the primary conducting system, makes increase in that

body impossible, and the premature activation of the cambium, which if it had not already resulted as a response to the physiological conditions prevailing, would now become a necessity. The ensuing development of secondary vascular tissue will follow the same course down to the petiolar base as in the normal root, with the exception perhaps that the dilatation of the pith accentuates the gap in the stele, but it is evident from the material examined that pith dilatation is unable to do any more than this, due to the resistance offered by the vascular system of the petiole. Once outside the petiole, however, conditions are altered. The slender system of the young root will be unable to resist the pressure exerted by the increasing pith, especially when it is taken into account that this latter tissue commences excessive dilatation when the root still consists of isolated xylem strands. Under these circumstances rupture of the cambium is easily effected, with its concomitant effect upon the outline of the stele. Now the root emerged from the petiole with an arc-shaped conducting system, into the interior of which arc the cambium had penetrated; as obviously this part of the cambium ring can stand more outward displacement than the other parts before rupturing, the break occurs elsewhere, and in each case examined has been at one of the two narrow ends of the now compressed stele. Hence the secondary tissue develops with a gap which is roughly at right angles to the indentation on the primary body lower down the root.

Given now a vascular system, incomplete, but with the potentiality of forming a complete cylinder, differentiating downwards round an expanding pith, the tendency will be for new cells formed from both of these tissues to be laid down, at the gap, in a direction resultant from two opposing forces —that of the cambium to form a cylinder and enclose the pith, and the tendency of the latter to keep the cambial cylinder incomplete. The new pith tissue continues to distend the stele, but is mainly proliferated across the gap and towards the cortex; in doing so it displaces and carries out with it the primary xylem and accompanying cambium which were situated at that corner. The result for the remainder of the cambium is that the end on the other side of the gap continues its course into the cortex (fig. 1, *cam.* 1): while at the other end (fig. 1, *cam.* 2) it continues its normal path round

the side of the stele and encloses the cambium (fig. 1, *cam.* 3) situated originally across the mouth of the arc. Due to these phenomena the stele therefore becomes hook-shaped. That the development of newly formed tissue in one direction more than another has also a physiological basis is seen when it is taken into account that round the outside of the young secondary stelar system, though no endodermis may be found, there occurs a fatty deposit. This will hinder the passage of material into the cortex from the conducting system on that side of the root, but on the other side, where no such barrier exists, diffusion will rapidly take place in that direction, and will be conducive to the intense meristematic activity which is seen there.

Considering now the region where the first signs of abnormal changes were observed in passing upwards from the tip, it was noticed that here the cambium had penetrated the cortex, in which tissue a tracheidal system was being formed. This condition occurs at the bottom of the gap in the cambium, a level down to which the formation of secondary tissue has not descended. In all probability the rupture in the cambium would occur over the whole length of the gap at the same time, and in both the longitudinal and transverse planes; hence the cambium would enter the cortex from the proximal and distal ends more or less simultaneously. The cambium above the gap forms secondary tissue, while the portion below forms a tracheidal system.

The net result of all this reorganisation of tissue, then, is the escape of material from the tissues of the stele across a gap formed by a rupture in that tissue, with the resulting increase in cellular activity around and outside that gap, the whole acting as a safety valve to relieve the pressure at that region. The continuance of this activity results in the alteration of the outline of the root, the newly forming tissue finally growing out as the swelling which gives rise to the adventitious buds.

That this swelling is produced from internal root tissue is obvious from the foregoing account, and is not a growth of callus, as stated by Taylor (2).

Initiation of the Bud.

In the region where the cambium had penetrated the cortex with the resulting differentiation of tracheids, it was noticed

that the cortical tissue surrounding these had become meristematic, a condition more pronounced in a small group of cells between the tracheidal system and the periphery. Closer examination of this group reveals the fact that the cell divisions are occurring according to a definite plan, so that it soon becomes organised into a bud, with two leaf papillae sur-

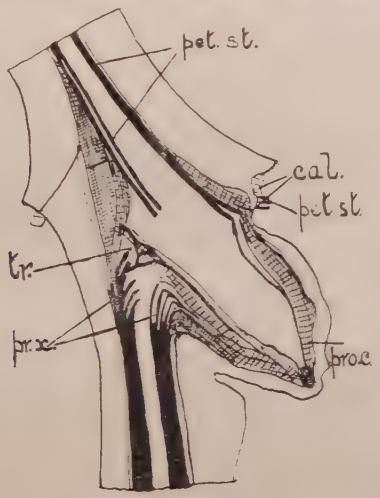

FIG. 2.—L.S. petiole and root showing origin of bud.

pet.st. = petiole strands; *tr.* = tracheids; *pr.x.* = remains of primary xylem at the gap in the primary system; *pro.c.* = procambium of bud; *cal.* = callus.

rounding an apical growing point and a differentiating procambial strand.

This bud is found on the side of the intumescence, which is still increasing in size, and with the vascular system of which the procambium of the bud is in continuity. A longitudinal section of a young stage of bud development shows that the procambium is united with the vascular system of the root on the proximal and distal sides of the gap; later on, however, when the swelling has attained a more considerable size, it is seen that the procambium has differentiated backwards into the pericycle of the petiole, so that at this stage the axes of this tissue and of the petiolar strand are in one straight line (fig. 2). At this period of development the bud grows downwards into the soil, and only later does it bend round and grow upwards. This is usually only the case

with the first shoot produced, the later ones as a rule growing straight outwards or upwards. This is possibly due to the fact that the first is being differentiated at the same time as the swelling is being formed, and is pushed downwards by the enlarging mass of tissue behind it, the later buds being initiated when the growth of the intumescence has slowed down.

The anatomy of the swollen region itself at this stage shows some interesting features, and deserves consideration in further detail.

It was seen in the region above that in which the bud initial was formed that rapid enlargement of the pith was concurrent with the formation of a hook-shaped sheet of secondary stelar tissue. The rapidly enlarging pith gives rise to the parenchyma of the swelling and is eventually traversed by the cambium, giving a continuous ring of conducting tissue.

This tissue in the lateral outgrowth differs from that in the root, however, in that in the latter the xylem is in a continuous mass of radiating rows, whereas in the former it consists of discreet strands (fig. 3, vi). All this tissue being produced from a cambium, the maturation of its lignified elements is in the centrifugal direction; the phloem, moreover, is collateral with the xylem. In other words, these discrete strands are typical stem strands, and it is to them that the conducting system of the shoot is united. In function, therefore, they must be considered as primary tissue, although they are derived from a cambium which at the same time is differentiating secondary tissue in the same transverse plane.

That this secondary tissue belongs to the root proper is seen by a series of transverse sections cut from this region downwards (fig. 3). The construction of the root stele beneath the swelling shows the peculiar feature of having a transverse section in which all the xylem is maturing in the centrifugal direction, and is collateral with the phloem instead of alternating with it. The gap in the system has not yet closed in, and a piece of cambium enclosed as previously described is forming inverted vascular tissue round the periphery of the pith; in this case phloem as well as xylem has been noticed.

It is obvious now that the vascular system of the swollen outgrowth is interpolated between true root-conducting system

and that of the young shoot. With the latter it is connected directly, the conducting tissue simply contracting and running out into the stem (fig. 3). The union between the conducting

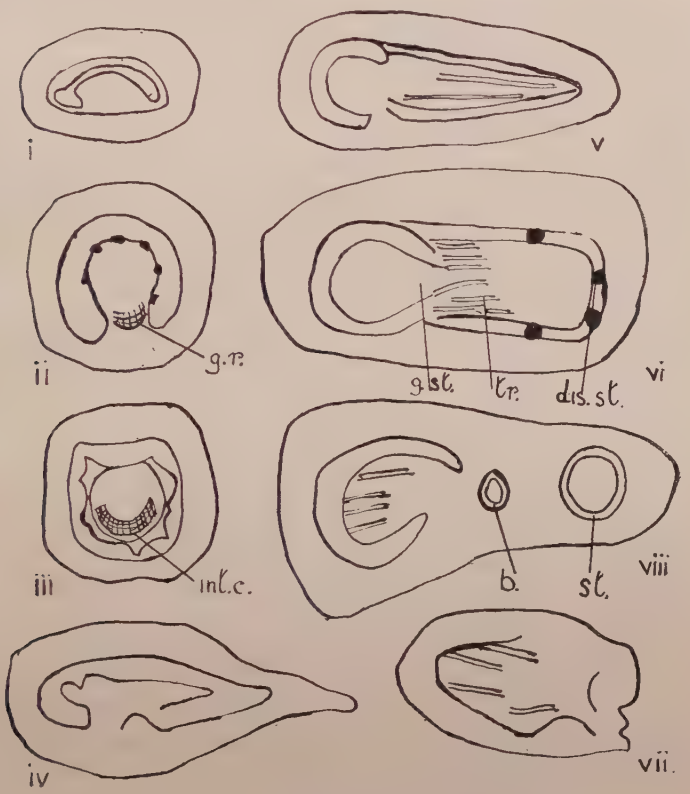

FIG. 3.—Union of vascular systems of shoot and root.

i, ii, and iii. Closing of gap in conducting system of root below emergence of bud, and inclusion of internal cambium. iv, v, and vi. Union between conducting system of shoot and that of root. vii and viii. Above the level of the last three.

int.c.=enclosed cambium; *g.r.*=gap in root system corresponding to indentation in fig. 8; *g.st.*=gap in the conducting system where the cambium enters the cortex; *tr.*=tracheids; *dis.st.*=discrete strands of stem; *st.*=stele of stem; *b.*=stele of second bud.

elements of the swelling and those of the root is not continuous throughout its length, complete continuity only occurring where the elements in the outgrowth run out into the shoot. Above and below this a gap occurs. Where the conducting system of root, swelling, and stem are continuous, the latter

two are oblique, or at right angles to the former, and in this region a considerable number of tracheids run longitudinally across the interior of the conducting system (fig. 3). These are probably only temporary in function, playing no part in the construction of the permanent tissues formed.

The union between other buds is precisely the same, their own proper vascular system uniting with the system of discrete strands in the intumescence.

An unusual feature is seen in a root produced from a petiole which has been split longitudinally. The base of the root abuts on the two cut ends of the half ring of the petiolar strand, from each of which a separate vascular system grows down into the root, thus providing the latter with two quite distinct steles.

After the complete union between shoot and root has been effected and the shoot has expanded its leaves, an absciss layer is formed across the base of the petiole, proceeding from the cortex inwards. When this layer is complete the leaf withers away.

Recapitulating now the outstanding anatomical features of this proximal region of the root, it is seen that here the primary system of the root disappears, and is replaced by tissue which matures centrifugally and is in continuation with the stelar tissue differentiating downwards from the base of the petiole. On one side of the swelling the tissue is continuous: on the other side it consists of discrete collateral strands; in other words, this region is one in which true root structure becomes transformed into true stem structure.

An interesting comparison can be made here between such changes and those occurring in the hypocotyl of the seedling. In the young tap root the initiation of the vascular system is by the formation of two strands of protoxylem. As the root tissues mature, the metaxylem is deposited laterally on either side of the protoxylem, so that in passing from the distal to the proximal part of the root increase of the xylem tissue takes place mainly in the tangential direction. The metaxylem is developed centrifugally. Towards the basal end of the root a transverse section shows two plates of xylem separated by a pith, each plate consisting of a small central portion of protoxylem flanked on either side by a much

larger triangular-shaped group of metaxylem. In this condition the conducting system enters the hypocotyl, in which region the protoxylem diminishes and finally disappears, and the four groups of metaxylem move apart and finally arrange themselves in four equidistant tracts. The anatomical transition is illustrated in fig. 4. The cotyledons are sessile.

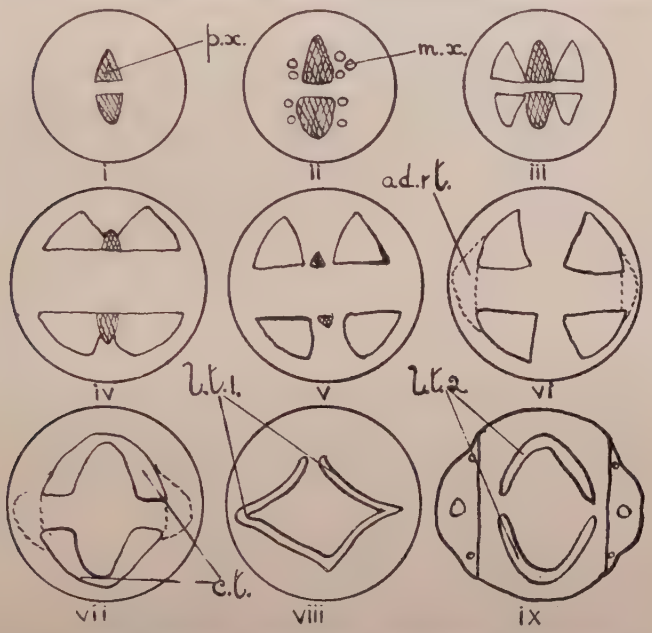

Fig. 4.—Transition from root to stem anatomy in seedling.

p.x. = protoxylem; *m.x.* = metaxylem; *c.t.* = cotyledonary trace; *l.t.* 1 = trace of first foliage leaf; *l.t.* 2 = trace of second foliage leaf; *ad.rt.* = adventitious root.

i. Behind root tip. ii–v. Decrease in protoxylem and increase in metaxylem, passing upwards. vi. In hypocotyl. vii. Intrusion of cotyledonary traces. viii and ix. Above hypocotyl.

The single cotyledonary strand after entering the main axis bifurcates, and each half remaining in the cotyledonary plane pursues a downward course, and becoming the metaxylem of the root unites laterally with the protoxylem, as described.

The essential features of the transition are:—

1. The reduction and final disappearance of the protoxylem of the root passing upwards to the base.
2. The continuation downwards of the cotyledonary traces as the metaxylem of the root; in the hypocotyl this

tissue completely replacing the xylem poles of the root.

3. The centrifugal maturation of these elements in the root.

The resemblance between these structural changes and the essential stages of bud production as described is obvious. Objection may be taken to the fact that in the one case, that of the seedling, all the tissues under consideration are primary, whereas in the other, secondary tissues enter into the structure of the body. That this is of no significance, however, is seen by the fact that at one stage the primary body and the secondary are both derived from the same tissue, namely, the cambium, and hence the distinction between the two types as far as their origin is concerned cannot be of any value.

Looked upon from the structural point of view, these new tissues form the foundation of the stelar system of the new organs regenerated, and therefore in function must be regarded as primary.

It is not unreasonable, therefore, to look upon this swollen portion of the root as a region whose internal construction is analogous to that of the hypocotyl, both functioning as regions in which the alternating xylem and phloem tracts of the root become the collateral strands of the stem, and in which maturation of the first lignified elements of the primary body alters in direction from centripetal to centrifugal.

As far as regenerative properties are concerned, this intumescence also suggests a region intermediate between stem and root, notably in the lack of polarity shown in the production of adventitious buds. Such lack of polarity is the characteristic feature of the tuberous swelling regenerated from a leaflet of *Zamioculcas*, one of the Aroideae, an organ for which the term "protocorm" has been suggested.

Now in the seedlings of this family the tubers have their origin in the hypocotyl, a fact which appears significant if considered along with the case of *Acanthus*.

The question of polarity in plants in general may be considered thus: On the shoot the adventitious buds are usually produced on the distal end and the roots on the proximal, while on the root the buds are usually on the proximal and the roots on the distal. In the case of the swollen structure on the *Acanthus* root, however, buds are produced freely all

over the surface, indicating that in this region the factors causing the difference in polarity between root and shoot counteract one another.

If this region really shows an analogy with the hypocotyl, it would be expected that in this latter part of the axis a similar lack of polarity should be seen in the regeneration of new growths.

Attempts to regenerate new growths from the hypocotyl in *Acanthus* have so far not been made, and therefore it is not possible to discuss the problem further in the case of this plant. Priestley and Swingle (1), however, have shown that, in plants in general, adventitious buds occur more freely on the root than on the hypocotyl, and more freely on the hypocotyl than on the epicotyl, suggesting again that from the point of view of regeneration the hypocotyl is intermediate between shoot and root.

Owing to lack of more evidence on this subject this discussion must be terminated with the suggestion that in propagation from the leaf of *Acanthus* not only root and shoot, but a region resembling hypocotyl, are regenerated—in other words, a return to a seedling-like condition has been effected.

Summary.

1. An isolated leaf of *Acanthus* planted under suitable conditions regenerates a root, of pericyclic origin, from the base of the petiole.

2. The internal construction of this root is normal only for a very short while. A rapid series of anatomical changes occur, principal among which are the destruction of the primary vascular system and the premature onset of secondary changes; the former being accompanied by rapid dilatation of the pith.

3. These changes lead to the outgrowth of the cortex as a swollen region on one side of the root, on the periphery of which bud initials are laid down.

4. This swelling is penetrated by the vascular system of the root, but here all root anatomy is lost, the vascular strands being typical stem strands; to these the conducting systems of the buds are united.

5. A comparison between the series of changes and those

occurring in the hypocotyl of the seedling is made, and an analogy between the two shown.

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(1) Priestley, J. H., and Swingle, C. F.: Vegetative Propagation from the Standpoint of Plant Anatomy. Tech. Bull. 151, U.S. Dept. Agric., Washington, 1929.

(2) Taylor, G.: The Origin of Adventitious Growths in *Acanthus montanus*. Trans. Bot. Soc. Edin., xxix (1926), 291.

The Scottish Alpine Botanical Club Excursion, 1932.

By Robert Moyes Adam, F.L.S. (With Pls. VI–VIII.)

(Read 16th November 1933.)

The south-western corner of Ross-shire, and where that county meets Inverness-shire amid the mountains, was the venue of the Club. Headquarters were sought at Cluanie Bridge Inn, but the discovery that the accommodation of that pleasant hostelry was limited made it necessary to seek farther afield. After considering the proximity of another centre, the Inn at Tomdoun in Glen Garry was selected, and there ample accommodation was found to house the party, and incidentally provided the Club with the comforts of a good house. The same hotel appeared to be a popular halt for road folk passing to and from Skye, and this was manifest during the Club's sojourn. Much was also seen to indicate the increasing flow of visitors towards this part of the Western Highlands.

It was on the evening of 15th July that the Club took up residence, the members having made the journey by devious routes. Motors brought half the company by Newtonmore and Dalwhinnie, while others travelled by train to Invergarry, and completed the journey from that point by car through Glen Garry. The same evening a consultation was held and an excursion programme submitted for the meeting. The President reported that he had been in touch with the tenants of the properties in the area—Charles Williams, Esq., M.P., of Glen Quoich, and Mr. Wilkie of Cluanie Lodge—and had from these gentlemen full permission to explore the hill country. The President also stated that due acknowledgment had been made for these favours, and an expression of thanks sent on behalf of the Club.

Thus on 16th July, after an early start, the Club party made their way to Cluanie Bridge in cars. Weather at the start did not promise very well, and later in the day considerable rain interfered with the plans and necessitated a curtailment of the programme. The run from Tomdoun was a pleasant affair, and in the ascent of the pass which rises

to 1424 feet delightful glimpses were obtained of the wild country at the head of Glen Loyne, and of the peaks of Glen Quoich Forest.

The slopes are mainly grassy, and except in the low ground present remarkably green sides. In Glen Loyne a chain of interesting lochs link up to form the river of that name, which, after a flow of a few miles, enters the Moriston in Glen Moriston.

Beyond the summit of the pass, where the sharp descent commences towards Glen Cluanie, a further mountain panorama greeted the party. From this elevated view-point the great ranges of the Ross-shire Alps unfolded in every direction. Their great green sides were a notable feature, while the dark-hued tints of heath land were conspicuous by their absence. Notice was taken of the Inn at Cluanie Bridge. In the distance it looked like a solitary white speck in the landscape, just discernible at the base of giant heights, and built where our winding track from the pass met the road from Glen Moriston in its westward trend to Glen Shiel. At Cluanie Bridge the Club transport was left behind and steps turned toward the north side of the Glen. The weather prospects had now become distinctly gloomy. A heavy curtain of wet mist, accompanied by a drizzling rain, obscured much of the tops, which half an hour before had been clear of cloud. It was now a day for a compass and a definite plan. The objective was Carn Fuaralach, a summit of 3241 feet, a modest height among the group of surrounding bens, but its geological character was expected to present the alpine botanists with the quarry they were in search of.

The south face of this hill, like its neighbours, fell smoothly and steeply to Cluanie, and one saw few outcrops of rock to relieve the monotony. This surface was accounted for by the angle of slope coinciding with the general strike of the underlying rocks. It was a feature in marked contrast to those prevailing on the north side of this range. There one met with a series of inclined folds of schist abruptly broken, and forming a range of shattered cliffs of very unstable rock: it was to this scene that the Club had set its mind and hoped to reach and visit in the course of the day.

A long and stiff uphill pull from Cluanie brought the party into close contact with the great, green, treeless slopes.

Loch Garry. A view of the eastern end, showing the surrounding woods of birch and occasional Scots pine. In the foreground deforested slopes are densely overgrown by bracken, while in the distance can be seen the heights of Glen Quoich forest.

The absence of definite heath was notably evident on all sides. There was no lack of peat soil, and, over the water-logged areas, deer grass tussocks dominated. In some places a series of peat hags showed stages of disintegration, but, over all, there appeared much proof that the slopes were a valuable grazing, and, although part of a sheep-run, carried large herds of Red Deer. The domestic animals, we were informed, however, during the sporting season were removed to other pastures.

Shortly after the ascent had commenced, the Club party divided. One section kept to the lower ground, while the second took the higher levels. In the course of the day much ground was covered, and eventually the summit was reached. It was found to be a grass-covered ridge with a dense crop of *Vaccinium Myrtillus* mixed with the pasture. *Alchemilla alpina*, which is so characteristic a member of the summit flora in the Breadalbane Hills, was here noted to be rare. From the summit a descent was made in a north-easterly direction. The ground, on this side, was found to be much steeper, and rocky. An attractive face with wet rocks, about 500 feet down, revealed a small array of alpines. *Potentilla Sibbaldi* was most prominent, and densely carpeted the slope. At some distance farther down, and on the steep earthy slope of a stream gorge, the most interesting find of the day appeared in the shape of *Gnaphalium sylvaticum* var. *nigrescens*. At another point in a deep ravine vigilant eyes caught sight of a clump of the polydactylous form of *Lastrea Filixmas* var. *abbreviata*, and, with difficulty, a handsome portion of this fern was removed for cultural purposes. Another fern, picked on the same slope, was the *furcans* variety of *Blechnum Spicant*. Towards 7.30 p.m. the parties rejoined at Cluanie and motored back to Tomdoun, a journey which was enlivened by the sight of an unfortunate motor-car which had gone into a bog at the roadside. This mishap had blocked the road; but in half an hour, and after rendering assistance to salvage the machine, a passage was made possible and Tomdoun reached without further incident.

On the morning of the 17th, cars were again requisitioned and used to carry the company to Loch Quoich. The region to be explored lay around the lodge and close to the loch shore. Loch Quoich is an expansive sheet of water, over 6 miles

in length, and is surrounded on all sides by lofty hills. To many, the region is notable for the excessive rainfall recorded. Outstanding among the records is one of 180 inches, being the measured amount which fell in the course of a year. There is also a 24-hour period, when upwards of 6 inches was recorded, constituting a record for any part of Scotland. This occurrence, which happened in October 1920, carried away quite a hill-slope and demolished a stalker's house with loss of life. The scene of the disaster is still visible as a scar on the slopes at Coire Bhuide. It was, therefore, not a little significant and remarkable that the Club should enjoy fine weather in such a spot. Some rain actually did fall, though the amount was trifling, but it bore out the local opinion that some rain falls every day.

Around Loch Quoich, on the north side, some fine Larch forest was observed, and some of the poles were noted for their size and straightness.

Towards the western extremity, at the entrance to Glen Hourn, a derelict plantation of Scots Pine showed signs of ill-health on a water-logged site. Heather is by no means a dominant plant in the area, its place being taken by characteristic grasses of West Highland slopes, which are accustomed to excessive rainfall. Of these *Aira caryophyllea* and *Deschampsia caespitosa* are plentiful, the latter species rarely forming its typical clumps. *Molinia coerulea* is abundant and was seen exhibiting very variable character. *Poa annua* was observed as high as 2000 feet, and nearly all the plants of *Festuca duriuscula* showed stages of vivipary. Among other grasses *Sieglingia decumbens* and *Koeleria gracilis* var. *britannica* were numerous on the lowest slopes. It might be said that much of the low ground of the valley about Tomdoun and towards Loch Garry has quite good pasture. On the slopes there is much natural wood of oak and birch, and on the southern aspects of the Glen a considerable sprinkling of Scots Pine of great age. Part of this area has been acquired by the Forestry Commission, and planting has been begun. Over the length of Glen Garry there is much evidence of a one-time crofting population. In recent years, however, this has dwindled down to one or two small farms. Some areas around Loch Garry, recently stripped of forest, are now infested with bracken, and so high and dense are the plants

The view to the north from the summit of Aonach air Chrith (3342 ft.). The sharp cone of A'Chioch forms the foreground. In the distance are the summits of West Ross with a general level above 3000 ft. Sgurr nan Ceathreamhnan, the highest peak on the horizon, rises to 3771 ft.

as to make a passage impossible. Beside Tomdoun, the attractive Loch Poulary was visited. This sheet of water is really a broadened stretch of the River Garry. The water is shallow, and has a vegetation typical of the Highland loch, *Lobelia* and species of *Scirpus* round the margin.

On the 18th Cluanie Forest Hills were again selected for investigation, Aonach air Chrith, the big hill which attains 3342 feet and frowns down on Glen Cluanie in the south side, being the chosen ground.

It was a morning for the gods, as a member put it, when the party set out. Warm sunshine bathed the landscape, and on the way a halt had to be called to view again the scene from the summit of the pass. On this occasion the visibility was perfect, and the memory remains of a sea of summits standing out with crystalline sharpness as far as the eye could reach.

The cars were again safely parked at Cluanie Inn, and soon thereafter the party were fording the River Cluanie and crossing a wide stretch of alluvial land and on to the steep face beyond.

The hills on the south side of Glen Cluanie correspond in character to the heights to the north. Their southern slopes are comparatively smooth, while the northern sides are flung down abruptly to form a wild series of corries.

It was to the great northern corry of Aonach air Chrith that the Club made their way, and to make a more thorough examination the party divided its forces. One section took the shoulder of Druim Shionnach, while the other plodded along the stream course that debouched from the corry. A complete absence of trees, except for an occasional Mountain Ash, made for rather a deserted scene, but in the hollows an occasional plant of interest was noted. The cliffs which lay ahead looked formidable, but on closer acquaintance proved accessible. Numerous gullies attracted attention, and in some of the ravines much time was spent. Water issued sparingly from the rocks, but only in a few select corners were conditions furnished for rich vegetation. The greater portion of the cliffs was found to be exceedingly dry and barren of plant-life.

Slowly but surely the ascent progressed, but the "bag" of plants was light. Once the top of the ridge was gained a very different aspect of the mountain met the eye. Here,

green and grassy slopes, and an easy gradient, rolled away towards Glen Loyne—a pleasant contrast after the rocky scenes encountered during the climb up. From the point in the corry where the party emerged the summit and highest point of Aonach air Chrith lay to the right and rose gracefully another hundred feet or so above the general level. Grassy slopes clothed the top, except to the north, where it projected and formed a minor cone with sides that fell sharply down. This feature of the mountain appears as the conspicuous landmark in the mountain outline when seen from Cluanie.

The cairn claimed a long pause, for the view was one of the most impressive and extensive seen in the course of Club climbs. Ben Nevis could be seen dominating the ranges of the south, while Mam Sodhail and Beinn Fhada did the same for the northern horizon.

Indeed, the identification of mountains led to much discussion and speculation, so vast and puzzling was the panorama spread out in all directions. The view also provided among other points a splendid example of the dissected tableland that composes this western tract of Highland territory.

Eventually the descent was reluctantly begun, some members taking the corry immediately below the summit. Others elected to traverse towards the top of Druim Shionnach and survey the summit of this peak. Much of the area covered consisted of mountain-top detritus, very dry and barren.

Finally the respective parties left the hill and reassembled about 7 p.m. at Cluanie, where, after a light refreshment, they resumed the road journey to Tomdoun.

The morning of the 19th saw the departure of some of the party, and the remainder proceeded by Invergarry and Gairlochy to Loch Arkaig. At the point where the Allt Mhuic enters the loch a halt was made and a search made in the immediate vicinity. On the shingle by the loch side a very fine pink form of Bladder campion was collected. Much of the Arkaig slopes held oak forest, and woodmen were busy cutting out the oldest and biggest trees. The road consequently was rather difficult to negotiate, but the party suffered no mishap. On the return run some time was spent on the slopes above Loch Oich, where the hill has been cleared of its timber. Rain interfered with the outing, but not sufficiently to spoil the day.

Potentilla Sibbaldi Hall. f. Wild plants growing over wet rocks, eastern corrie, Carn Fuaralach.

Calluna vulgaris Hull var. *incana* Reichb. Wild plant in flower among undergrowth of Scots pine wood at Blackhills, Moray.

Robert Moyes Adam.

The 20th saw the break up of the meeting, the members going their respective ways. Two, who journeyed to Blackhills, Moray, spent an interesting time in that garden. In the course of the visit an unusual heath, *Calluna vulgaris* var. *incana*, was found plentifully in the pine woods at Blackhills. This is the form clothed with dense woolly hairs frequently found in Northern Scotland.

The garden at Blackhills, which is the work of its owner, Mr. Christie, was a most delightful one to visit. The rockwork and the woodland were exceptionally fine. Some fine groups of Meconopsis and Foxgloves, with many new Chinese species of Primula, were seen and admired. The lake at Blackhills, too, proved most attractive. The whole margin was occupied by a variety of aquatics, among which water lilies were the chief. The same garden was found to have a host of ornamental shrubs, and the time was all too short to see in full the wonders of Blackhills. The hospitality of Mr. Christie was lavish, and reluctantly in the afternoon of 21st July, after acknowledging his kindness, car was boarded, and, after a speedy run, Edinburgh was reached in the evening, thus terminating a meeting which will be remembered for the variety of interests explored and pursued.

Among the more interesting plants seen were the following: *Thalictrum alpinum* Linn., *Trollius europaeus* Linn., *Nymphaea* (cultivated sp.), *Cochlearia alpina* Wats., *Linum catharticum* Linn., *Geranium pratense* Linn., *Rubus saxatilis* Linn., *Potentilla Sibbaldi* Hall. f., *Alchemilla alpina* Linn., *Saxifraga stellaris* Linn., *S. aizoides* Linn., *Parnassia palustris* Linn., *Sedum roseum* Scop., *Drosera anglica* Huds., *Epilobium anagallidifolium* Lam., *Cornus suecica* Linn., *Solidago Virgaurea* Linn. var. *cambrica* (Huds.), *Antennaria dioica* Gaertn., *Gnaphalium sylvaticum* Linn. var. *nigrescens*, *G. supinum* Linn., *Hieracium alpinum* Linn., *Lobelia Dortmanna* Linn., *Vaccinium uliginosum* Linn., *Azalea procumbens* Linn., *Trientalis europaea* Linn., *Veronica humifusa* Dickson, *Polygonum viviparum* Linn., *Salix herbacea* Linn., *Goodyera repens* Br., *Gymnadenia conopsea* Br., *Juncus trifidus* Linn., *Rynchospora alba* Vahl, *Juniperus nana* Willd., *Athyrium alpestre* Milde, *Lastrea aristata* Rendle et Britten var. *alpina*, *Lycopodium alpinum* Linn.

The Cytology of Lonicera deflexicalyx Bat.

By T. W. Brown, B.Sc.

(Read 16th November 1933.)

The material for this investigation was provided by a plant grown in the Royal Botanic Garden, Edinburgh.

The technique adopted consisted in abstracting the anthers from the flower bud and crushing them on a slide. The smear so obtained was fixed in "2BE" (La Cour 1931). The fixing and staining schedule as outlined by La Cour was followed, the stain used being Gentian Violet. In *Lonicera deflexicalyx* n = 9.

Pollen Mother Cells in all stages of meiotic division were observed, though difficulty was experienced in interpreting the prophase stages of the Heterotype division. Nothing unusual about the Meiosis of *Lonicera deflexicalyx* was observed except the occurrence of a single pair of lagging chromosomes. This homologous pair were noted in a Pollen Mother Cell at late anaphase stage of the homotype.

Yen-An (1933) reports the presence of centrosomes in *L. alpigena*, *L. Xylosteum*, *L. Caprifolium*, *L. Glehnii*, *L. myrtilloides*, and of asters in *L. alpigena*.

Neither asters nor centrosomes were observed in *L. deflexicalyx*, though Pollen Mother Cells were examined at all stages.

My thanks are due to Dr. Alexander Nelson for guidance given throughout the course of this study.

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TRANSACTIONS

OF THE

BOTANICAL SOCIETY OF EDINBURGH

SESSION XCVIII

Anatomical Features in the Roots of the Genus Primula. By John Murray, B.Sc.

(Read 15th June 1933.)

Publications on the Primulaceae show that little research has been carried out on the roots of the genus Primula. Decrock (1901) investigated the general anatomy of the Primulaceae, but only examined the root anatomy of a few species of Primula. Since the beginning of this century, however, many new Primula species have been introduced by collectors, and little anatomical investigation has been carried out on these. The taxonomic arrangement of the sections in their phyletic sequence, as propounded by Pax, later by Professor I. Bayley Balfour, and recently modified by Professor Sir William Wright Smith and George Forrest, has been used in this study as the most convenient for reference.

All the roots selected for examination were taken from growing plants, one to five years old, representing as many sections of the genus as are found in cultivation. Transverse sections were prepared from the mature parts of the roots, and an investigation made of the anatomical features.

The tegumentary system of the mature root, which shows much variation in structure, is found in most species to be of two layers, a piliferous layer and an exodermis. Many

species growing under optimum conditions show the cells of the piliferous layer prolonged into short hairs as found in the well-known species *P. acaulis*, *P. vulgaris*, and *P. veris* of the Vernales section ; but others are destitute of hairs, a condition frequently associated with species growing in moist regions, as found in the species examined belonging to the Amethystina, Muscarioides, and Candelabra sections. *P. Auricula*, *P. Palinuri*, and *P. marginata* of the Auricula section are provided with hirsute roots which show an interesting xerophytic feature, the hairs themselves being lignified to prevent desiccation as the roots are often partly exposed in the crevices of limestone rocks.

An exodermis consisting of isodiametric or radially elongated thin-walled parenchyma cells is characteristic of most species except *P. Rusbyi* of the Nivales section and the Auricula species *P. Palinuri* and *P. Auricula*, which have their cell walls suberized, while *P. macrophylla* of the Nivales section has its large round cells rich in tannin, all features for the prevention of desiccation.

The cortex is another layer which shows much variation in structure. The species examined of the Megaseaefolia and Vernales sections present uniform isodiametric thin-walled parenchyma cells as found in most herbaceous roots. The outer cortical zone in *P. grandis* of the Grandis section, *P. auriculata* of the Farinosae section, and *P. macrophylla* of the Nivales section is composed of thick-walled collenchyma cells, while in *P. florida* of the Souliei section the cells are sclerenchymatous. In *P. Kingii* of the Amethystina section, *P. capitellata* and *P. auriculata* of the Farinosae section, and *P. Poissonii* of the Candelabra section a central cortical zone of aerenchymatous tissue is observed, a correlation with species growing in damp localities. *P. florida* of the Souliei section and *P. yunnanensis* of the Farinosae section, species found in the cavities of perpendicular limestone rocks, show deep staining contents in the cortical cells, and illustrate well the mural pits with protoplasmic connections to neighbouring cells. The parenchyma cells of the central zone in the species examined of the Denticulata and Capitata sections have an irregular shape, presenting a crushed appearance. In all species examined the inner cortical zone is made up of isodiametric or rhomboidal parenchyma cells arranged in con-

centric circles and radiating rows. This arrangement in *P. Beesiana*, a Candelabra species, is so symmetrical that the whole cortex may be likened to a geometrical design.

The endodermis in most species is composed of oval cells with suberized radial walls, except *P. auriculata* of the Farinosae section and *P. grandis* of the Grandis section, which differ from the others in having their endodermal cells divided radially into two divisions, thus presenting evidence of a common feature. Decrock describes in the species *P. Auricula*, *P. bullata*, *P. verticillata*, and *P. sinensis* peculiar endodermal cells, tangentially elongated and radially divided into several divisions with heavy depositions of suberin, and exfoliation of all tissues external to the endodermis, but in this investigation similar features have been found in all species examined belonging to the sections Cortusoides, Obconica, Sinenses, Malacoides, Bullatae, and Verticillata.

Those species having much divided endodermal cells are also the only representatives which show development of secondary tissues in the vascular cylinder, a correlation with their growth in crevices or on the ledges of limestone rocks. In the Bullatae species *P. Forrestii* and *P. redolens*, and the Verticillata species *P. verticillata* and *P. floribunda*, the secondary xylem is formed in broad cuneate bands, extending from the polygonal-celled medulla to the cambium, with alternating medullary rays of tangentially divided parenchyma cells. Except for these woody types, the vascular cylinder in every species is typical of herbaceous roots with two to eleven exarch xylem poles. The pith is composed of a narrow or broad zone of isodiametric or polygonal parenchyma cells.

Based on these anatomical features, groupings of the species in the genus Primula can be made which show a close agreement with the taxonomic sections. The peculiar anatomical features present in certain species may form a valuable aid to the taxonomist in his determinations of relationship where this is doubtful.

In conclusion, the writer expresses his thanks to Professor Sir William Wright Smith for facilities for study in the laboratory; for permission to obtain root material from the valuable Primula Collection in the Royal Botanic Garden, and his continued interest during the investigation.

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Leaf Development and Vegetative Propagation in Kalanchoe tubiflora. By Gertrude Clamp, Ph.D. (With Pl. IX.)

(Read 19th April 1934.)

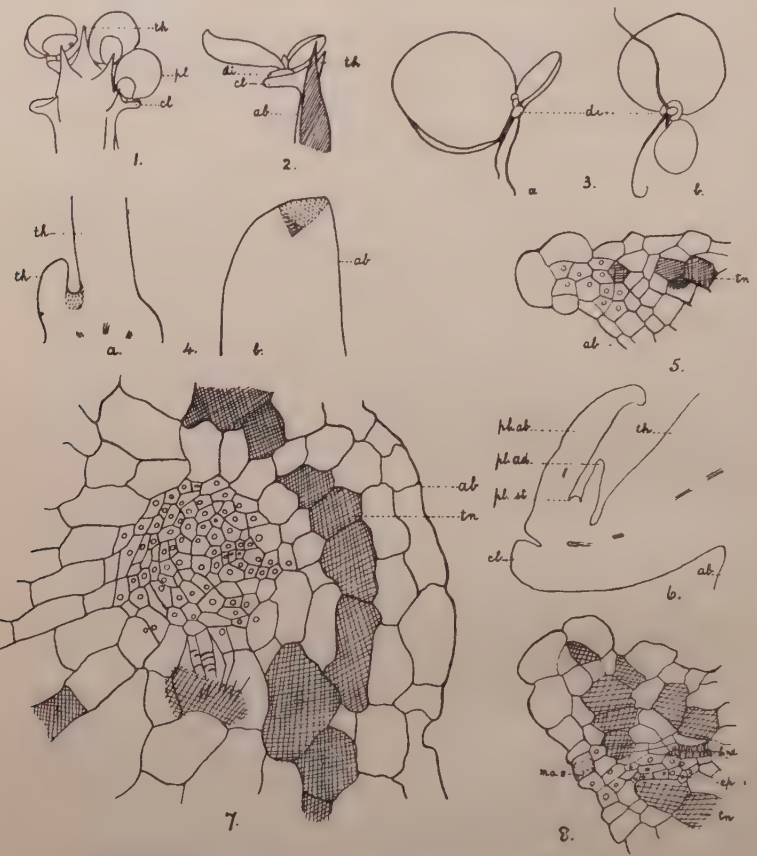
Introduction.

Kalanchoe tubiflora (Harvey) Hamet, a member of the Crassulaceae, is a succulent plant native to Madagascar. It was collected and described in 1891 by Elliot (4), under the name *K. verticillata*. In 1912 Hamet (7) published the record and synonymy of this plant, which he named *K. tubiflora*, and thus it figured in Curtis's Botanical Magazine (3). One of the most interesting features of the plant is the method of propagation which it exhibits, a short note on which was published in 1929 by Baron, Graham, and Stewart (1). The nomenclature adopted in that note is adhered to in the present paper, except that the term "plantlet" is used in preference to that of "bulbil" to denote the regenerative shoots.

The material used in this investigation was taken from greenhouse-grown plants in cultivation in the Cruickshank Botanic Gardens, Aberdeen. The adult plant has a long, slender main axis, which branches infrequently and bears numerous leaves throughout its length. These are inserted spirally, but are apparently in whorls of three, in the upper part of the axis, since only each third internode is elongated (1·5–3 cm. long). The leaves are sub-cylindrical, 4–5 mm. wide, 7–7·5 cm. long, slightly constricted at the base, and have a shallow groove along the adaxial surface. The leaf-tip is terminated by a number of small conical teeth (often 5), of which the median is the longest. On the abaxial surface of the leaf protuberances extend outwards from between the teeth-bases to form the leaf-claws. When mature the leaf-claws are larger than the leaf-teeth, and each bears on its upper surface a regenerative shoot (or plantlet), which later falls to the ground and develops into a new individual (text-fig. 1).

When the plantlet is ready to fall from the parent leaf it consists, normally, of a short disc-like stem bearing two pairs

of leaves. The stem is not quite cylindrical, being more extended to the abaxial side and bearing the leaves nearer



1. Leaf-tip showing teeth, claws, and plantlets (front view). ×2.
2. Half leaf-tip (side view), with plantlet in position. ×2½.
3*a*. Mature plantlet. ×3. 3*b*. The same, from below. ×3.
4*a*. Plantlet meristem as seen in L.S. parallel to adaxial surface of leaf.
4*b*. Plantlet meristem as seen in L.S. between leaf-teeth.
5. L.S. tip of plantlet leaf showing distended epidermal cells. ×260.
6. Diagram of L.S. plantlet on claw. ×26.
7. T.S. meristematic plate at base of plantlet. ×260.
8. L.S. tip of plantlet leaf showing hydathode. ×225.

ab = abaxial surface; b.nd = bundle end; cl = claw; di = disc; ep = epithem tissue; mo.s = modified stomatal cell; th = tooth; tn = tannin; pl = plantlet; pl.ab = plantlet abaxial leaf; pl.ad = plantlet adaxial leaf; pl.st = plantlet stem apex.

to the adaxial one. It is very short and merely forms a cushion of tissue by means of which the plantlet is in com-

munication with the leaf-claw, through which it derives its water supply until it falls from the plant (text-fig. 2).

The leaves of the first pair are very unequal in size, the abaxial one being 2–3 times as large as the adaxial. They are very different in appearance from the parent leaf, since they are spoon-shaped and have an entire margin which may be carried slightly forward to the adaxial surface at the tip of the leaf. They are, however, comparable to the parent leaf in being fleshy and sessile. Also the first pair of plantlet leaves lie in the same plane as the subtending leaf. The second pair of plantlet leaves are exceedingly small, being only just discernible at this stage. They are equal in size and are at right angles to the first pair (text-fig. 3, *a*). There is no development of internode between the first and second pair of leaves until the young plant begins to grow.

In nature there is probably no development of roots before the plantlet falls from its subtending leaf, but in the case of greenhouse-grown plants the plantlets produce a varying number of roots from the base of the stem, all, it has been observed, from the side towards the median tooth (text-fig. 3, *b*). Similarly, under cultivation the shoot of the young plant may begin to develop, and plantlets still attached to the parent leaf show an elongation of internode between the first and second pair of leaves, and a small stem apex between them.

An anatomical study of *Kalanchoe tubiflora* reveals that the general features of this plant closely resemble those of the other members of the Crassulaceae. Many of these features are correlated with the succulence of habit induced by the conditions of the habitat and are shared by other typical dune plants. Hence the peculiar interest of this plant lies not so much in its anatomical features as in its characteristic method of vegetative propagation.

Methods.

Material to be sectioned was fixed in formalin-acetic-alcohol or a weak chromo-acetic-acid solution. Serial sections were cut at 8–10 μ and stained with alcoholic safranin and picro-anilin blue. Various combinations were tested, but this was found to be the most satisfactory as it gave a differentiation

in both meristematic and mature tissues. In some cases material was examined in the solid after clearing with xylol.

Leaf Development.

Stem Apex and Leaf Origin.—The growing-point of the stem is confined to a short meristematic region at the tip. A dermatogen layer is clearly distinguished, composed of small, regular, rectangular cells with thin walls and large nuclei. Below this layer lie 2–4 layers of similar typically meristematic cells which form the cortical region. At the apex itself the cells of these layers are regularly arranged, but a little behind the true apex this regularity is lost, and it becomes impossible to trace the individual layers. Beneath the cortical cells are those forming the central cylinder. The limits of this cylinder are not sharply defined, but the cells of the region tend to be arranged in longitudinal rows, and most of them are larger and have less conspicuous nuclei than those of the epidermal and cortical layers.

Immediately behind the apical point of the stem a group of the cortical cells divides more rapidly than the remainder, forming an irregularly arranged mass of cells. The epidermal cells immediately over this area meanwhile are also dividing more rapidly to keep pace with the growth of the tissue below. A small protuberance—the leaf primordium—is formed in consequence of this growth. Thus the epidermis of the leaf arises from, and is continuous with, the epidermis of the stem, while the leaf mesophyll originates from a group of stem cortical cells.

Formation of Groove.—Cell-divisions in the leaf primordium proceed more rapidly than in the stem apex itself, so that the latter is soon overtopped by the young leaf. As development in this organ continues, the region of greatest meristematic activity becomes confined to the apex, while the cells of the basal region divide less frequently and become larger and vacuolated. The result of this apical meristematic activity is a growth in length far exceeding that in any other dimension. When the basal cells lose their highly meristematic appearance the abaxial cells enlarge earlier than the adaxial cells and attain greater proportions. The result of this discrepancy in cell size is that the marginal regions of the

leaf are pushed forward towards the adaxial surface, and in this way the adaxial groove is formed (Pl. IX, fig. 1).

Formation of Leaf-teeth.—When the leaf is barely 1 mm. long and one-third as thick, certain apical-adaxial groups of the apical meristematic cells divide more actively than the adjacent ones. As a result of these divisions a series of protuberances is formed in basipetal succession, including a terminal median one and a varying number of lateral pairs. The latter are marginal and borne towards the abaxial surface of the leaf. The cells in each of these protuberances divide repeatedly for a time without conforming to any definite arrangement. Conical processes are formed, which are about 18 cells long and 13 wide in the case of the median one, and somewhat smaller in the case of the laterals. At this point active division ceases and the cells gradually attain maturity. The processes so formed are the leaf-teeth, which undergo no further development (Pl. IX, fig. 2). Between the bases of these teeth groups of the original apical meristematic cells persist (Pl. IX, figs. 2 and 3). They retain their meristematic appearance, although there is no extensive development until later when the plantlet and claws grow.

In subsequent development increase in size of the leaf is due to the increase in size of the individual cells. When the cells of the leaf cease to divide actively they enlarge enormously to form the large irregular mesophyll cells of the mature leaf. The constriction observed at the base of the leaf is due to the cells of about four superimposed layers, which fail to enlarge to the same extent as the contiguous ones and are more rectangular in shape and more regularly arranged. They form the region of detachment of the leaf. [The development of the leaf-claws is described in conjunction with that of the plantlet, as there is no production of claws by the leaf independent of plantlets.]

Plantlet Development.

Origin.—The plantlet originates from certain of the cells in the meristematic group persisting between the leaf-teeth (see above). The other cells of this group contribute to the formation of the leaf-claw and its vascular supply. The shape of the meristematic group may be seen from the accompanying

diagrams (text-fig. 4, *a* and *b*). The meristem extends from the abaxial surface of the leaf inwards for 8–10 cells and is rather higher at the abaxial end. Between the teeth bases it is approximately 2 cells wide, and it extends for a short distance up the sides of the bordering teeth. It has a maximum depth of about 8 cells, decreasing suddenly on all sides except the abaxial, where it tapers gradually from the point of maximum depth.

The first cells of the group to show active divisions are those 4–6 cells most deeply situated (text-fig. 4, *b*). These divide to form a small compact group of cells, which elongate and presently differentiate into vascular elements. Differentiation proceeds further and further into the leaf tissues until connection is established with the vascular system of the leaf already functioning, and the necessary supply to the developing plantlet is thus assured.

Primordium.—Immediately above this group of 4–6 cells the meristem consists of 2–3 more or less parallel layers of cells covered by the epidermal layer. In these layers the adaxial cells divide more rapidly and give rise to the plantlet and part of the claw, while the abaxial cells are less highly meristematic and contribute only to claw formation. The adaxial cells divide repeatedly in an irregular manner, forming a protuberance in the same way as that in which the protuberances of the leaf primordia and axillary buds of the parent plant are formed. The plantlet primordium at this stage is very similar in appearance to the primordium of a young bud. General cell-division continues without any specialisation until the primordium has dimensions approximating to 10 cells in height and 15 cells in width (as seen in median L.S.). The abaxial side now grows more rapidly than the adaxial, and the primordium of the first leaf becomes distinguishable (Pl. IX, fig. 4).

Leaf Development.—The primordium of the abaxial leaf is large and occupies the abaxial-apical region of the young plantlet. It is followed almost immediately by the formation of the primordium of the adaxial leaf, which is much smaller. Both leaf primordia develop for a time by cell-divisions which are more rapid in the apical than in the basal cells. The apical epidermal cells become very much enlarged, being 4–8 times as large as the normal cells (text-fig. 5).

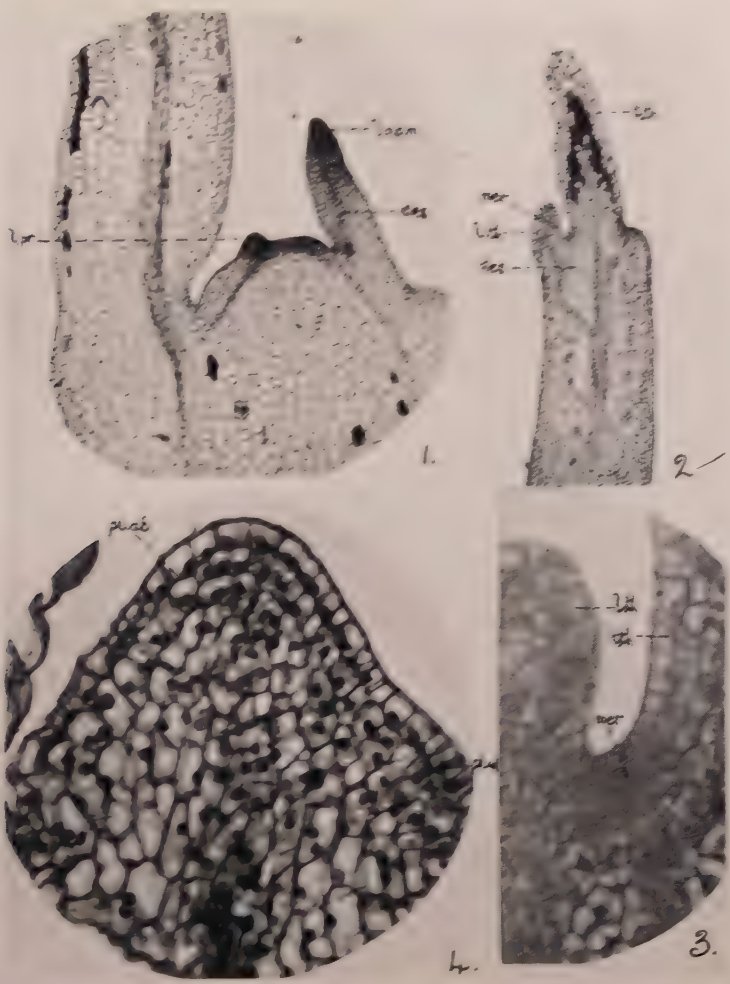


Fig. 1.—L.S. stem apex. ×52.
Fig. 2.—L.S. leaf-tip, showing two teeth. ×52.
Fig. 3.—L.S. lateral vein and base of terminal tooth with meristematic group between. ×450.
Fig. 4.—L.S. young plantlet. ×450.

l.pr = leaf primordium; l.ap.m = leaf apical meristem; des = desmogen strands; l.v = terminal vein; l.v.l = lateral vein; mer = meristem; ms = marginal sinus; pl.ax = plantlet axonal leaf primordium; pl.ad = plantlet adaxial leaf primordium.

Gertrude Clapp.

As the leaves become mature their cells increase in size and active division ceases. The abaxial cells mature before the adaxial and the central cells before the marginal ones. There is not so great a discrepancy in size between the ab- and the ad-axial cells as in the case of the parent leaf, and the margins are therefore not carried forward to the adaxial side of the leaf so markedly. Nevertheless, the abaxial epidermis is still somewhat longer than the adaxial. The flat expanse of the leaf-blade is formed by the continued meristematic activity of the marginal cells after the central ones have ceased to divide.

The Disc.—This is formed by the enlargement of the cells as the base of the plantlet primordium, which begins when the primordium of the abaxial leaf is laid down, and continues during the formation of the primordium of the adaxial leaf. The cells lose their meristematic appearance and cease active division. Subsequently the basal disc-cells are not able to expand equally with the others owing to the pressure of the contiguous claw cells. This causes a sharper distinction between the tissue of the plantlet and that of the claw than is shown during the earlier stages of development.

The Stem Apex.—After the primordia of the first two leaves of the plantlet are laid down a group of cells between them becomes conspicuous by reason of its highly meristematic appearance. Cell-divisions proceed for a time, and then development is arrested, leaving a small protuberant mass of meristematic tissue between the leaves. This forms the stem apex, and, subsequently, activity is resumed when the young plant begins to grow (text-fig. 6).

Claw Development.—When the divisions of the plantlet meristem cells begin, the leaf shows no sign of a claw, so that the plantlet formation proceeds ahead of claw formation in the initial stages. The stage at which claw formation is first indicated varies somewhat with the individual leaves, but occurs usually just previous to the formation of the abaxial leaf primordium. At this time the leaf shows a slight convexity of the abaxial surface at the tip, which is due to the general increase in size in the leaf-cells. When this increase in size takes place the plantlet primordium prevents the cells on the abaxial side of it from swelling adaxially, and a slight curvature of the abaxial surface results. Claw

formation thus begun is later continued by the division of cells at the base of the plantlet primordium. Here there is a plate of cells which divide more actively to the adaxial than the abaxial side, causing an excentric growth of tissue by which the growing region is carried out to the abaxial surface of the leaf (text-fig. 7). Normally, the result of such a growth would be an adaxial protuberance on the leaf, but in this case the bases of the leaf-teeth on the adaxial side of the plantlet primordium offer resistance to any growth in that direction. Therefore, by means of the new cells formed on the adaxial side, the plantlet gets carried further and further away from the teeth-bases, *i.e.* out on the abaxial surface of the leaf. This cell-division at the base of the plantlet primordium begins while the plantlet leaf-primordia are being laid down and continues during the development of the plantlet. The cells of the claw lose their meristematic appearance very soon after their formation and increase greatly in size—the adaxial cells being more elongated in the direction of the claw than the abaxial ones. Thus the claw tissue never appears to be generally meristematic, differing in this respect from that of the leaf-teeth. Though plantlet formation begins before that of the claw, the latter becomes externally observable much earlier than the former as a result of the much greater magnitude of the cells concerned. When mature the plantlet is the more obvious of the two structures, although the claw has by this time attained a size greater than that of the leaf-teeth.

General Anatomical Structure of the Mature Plantlet.

The disc has a stem-like structure although the general arrangement is excentric, the cortex being much wider on the abaxial side. There are four vascular bundles, of which that in the abaxial position is the largest, being about three times the size of any of the others. The bundles are more concentrated towards the centre of the organ, particularly in the base, than is the case in typical stems, and they enclose a relatively small pith.

The plantlet leaf, though very dissimilar in external appearance to the parent leaf, shows internally a certain similarity

in the character of the tissues. As in the adult leaf, the mesophyll consists of large, irregular, thin-walled parenchymatous cells, among which the small, ill-differentiated bundles are scattered. Large numbers of starch grains are present in the mesophyll cells of the plantlet leaves.

There is a further feature in which the plantlet leaf differs from that of the adult plant. The median bundle of the former terminates in a hydathode of the epithem type, while the latter possesses no hydathodes. The epithem tissue extends obliquely outwards from the bundle-end to the abaxial surface of the leaf, where it is in communication with a modified stoma (text-fig. 8). The latter consists of two cells with dense protoplasmic contents and a large nucleus, but no plastids. In some cases there is no water-pore between these cells, and it is doubtful whether the hydathode functions. Closely investing the epithem tissue are cells rich in tannin.

Discussion.

In the development of the leaf of the adult plant the formation of the claw is of outstanding interest. This is an unusual growth, which probably develops in consequence of the restricted space relationships of the growing plantlet and the leaf-teeth. It is conceivable that, if there were no leaf-teeth resisting growth to the adaxial side of the leaf, there would be no claw development, and the plantlets would be attached directly to the leaf margin. By means of the claw, however, the developing plantlet is carried out beyond the abaxial surface of the leaf and the restricting leaf-teeth, and is able to attain proportions which would otherwise be impossible. Nevertheless, the leaf-teeth do influence the structure of the plantlet, since they are responsible, to some extent, for the disparity in size of the first two plantlet leaves. The primordia of these leaves are laid down before the claw is fully developed, and therefore the adaxial side of the young plantlet is still confined between the adjacent teeth-bases. The abaxial leaf primordium, being laid down on the free side of the plantlet, is thus able to attain greater dimensions than the adaxial one. Once the primordia have been laid down, the larger one maintains its initial advantage, and the adaxial leaf consequently remains the smaller, even after the continued growth of the

claw has served to carry it out beyond the leaf-teeth. Since the second and succeeding pairs of leaves are of equal size it would seem that the inequality in size of the first pair is due to the mechanical influence of neighbouring structures, and is not an example of true anisophylly (Goebel (5)).

No evidence has been obtained as to the possible function of the leaf-teeth. Elliot (4) refers to the claws as broad reflexed teeth, but their development shows teeth and claws to be distinct structures. The latter are only produced in conjunction with plantlets, while the former are always developed on adult leaves, even on those which, for some reason, do not produce plantlets.

It is significant that Elliot makes no mention of the plantlets although he collected material in the field. On the other hand, his material had evidently borne plantlets, for he refers to a gland in the centre of the broad reflexed teeth, which is, in fact, the scar left on the claw by the detached plantlet. From this it seems that in nature the plantlets fall very early from the parent leaf. It is readily understood that under conditions of cultivation the plants are more protected, and that therefore the plantlets remain attached for an unnaturally long period of time. On this is based the view that under natural conditions the plantlets fall before there is any development of roots or extension of the stem. Even so, the plantlet is well equipped for starting an individual existence under adverse conditions. The enlarged apical epidermal cells are similar to the more extremely distended epidermal cells reported in *Mesembryanthemum crystallinum* and other xerophytic plants (Haberlandt, (6)). Such cells are used for the storage of water. Thus the plantlet has a reserve water supply, in addition to the general succulence of its habit, on which it can draw until its own root system is established. Similarly, it has a reserve of food material in the numerous starch grains present in the mesophyll cells.

The transitional leaves between the plantlet and adult plant leaves are worthy of careful examination. A study of the anatomy of these leaves would reveal the connection between the somewhat divergent vascular systems obtaining in the two leaf types. It might also bring enlightenment as to the significance of the hydathode in the plantlet leaf. As far as our present knowledge goes, it seems to be a rather anomalous

structure, the presence of which is difficult of interpretation. Again, it is from these transition leaves that evidence is to be obtained as to when the apical epidermal cells cease to become distended, and whether there is any correlation between these cells and the teeth formed in the adult leaf.

As a method of vegetative propagation this development of plantlets by *K. tubiflora* is almost unique. Among the naturally occurring methods referred to by Holm (8) that of *Bryophyllum* is the most closely approximating. The general organisation of the plantlet in both genera is very similar, since the plantlet of *Bryophyllum* consists of a short cylindrical axis, from which roots are produced, and two pairs of small leaves. Moreover, the plantlet originates from a group of meristematic cells in the notches of the leaf margin. There is, however, no suggestion of claw development, and the plantlets are produced with no definite regularity. In some accounts regeneration of the leaf of *Bryophyllum* is said only to take place when the leaf is detached from the plant (Loeb (9); Holm (8)), but other cases have been reported in which plantlets are produced by attached leaves (Braun (2)). Holm puts forward the view that, since the meristematic cells from which the regenerative shoots of *Bryophyllum* are produced are present in the normal leaf, even though plantlets are not always developed, these propagative structures should be regarded as something more than mere accidental or adventitious developments. This is much more markedly so in the case of *Kalanchoe tubiflora*, where the production of plantlets has become so stabilised as to form an integral phase of the normal leaf development. This stabilisation of plantlet production combined with the development of the claw and the differences in structure between plantlet and adult leaves make this method of vegetative propagation unlike any other of the recorded methods.

Although the plantlets afford the plant a means of multiplying far more readily than it would by seed-production, they have not entirely replaced reproduction by seed but provide an accessory method. Plants bearing plantlets have flowered and set seed from which healthy seedlings have been raised, bearing plantlets in their turn.

The writer wishes gratefully to acknowledge her indebtedness

to the late Professor W. G. Craib and to Dr. D. G. Downie for their suggestions and sympathetic interest throughout this work.

Summary.

1. *K. tubiflora* propagates vegetatively by means of regenerative shoots, or plantlets, developed at the leaf-tip, being itself a succulent plant native to Madagascar.

2. The mature plantlet is borne on the upper surface of a leaf-claw projecting abaxially from between the leaf-teeth. It consists of a short excentric stem-like disc bearing two pairs of leaves, the first pair of unequal size.

3. In the early stages the leaf is developed by an apical meristem, of which certain adaxial cell groups give rise to the leaf-teeth.

4. Meristematic cells persist between the bases of the leaf-teeth and by subsequent activity produce the claws and plantlets.

5. The young plantlet primordium is very similar to that of an axillary bud.

6. The primordia of the first plantlet leaves are very unequal in size, the abaxial being the larger.

7. The anatomy of the plantlet is, generally speaking, similar to that of the adult plant. The outstanding differences are in the leaf structure.

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Notes on recent Additions of British Mosses to the Collection in the Herbarium at the Royal Botanic Garden, Edinburgh. By William Young.

(Read 19th April 1934.)

In February 1932 I had the pleasure of submitting to the Society some "Notes on the Collection of British Mosses in the Herbarium." I then detailed an account of its origin nearly a century ago and related the manner of its growth during the years by contributions from those in charge of it—by gift and purchase from eminent botanists. It had gradually increased in bulk and importance, and included many thousands of specimens from all parts of the British Isles.

During the past two years several large collections have been received and incorporated into it. Many new vice-county records have been added to the Census Catalogue published by the British Bryological Society, and several desiderated species have been acquired.

The first large collection was presented by Mr. Robert M. Adam. It was formed by his brother Mr. James C. Adam, and consisted of several hundred specimens in fine condition named and mounted on regulation sheets of paper. There were 56 new vice-county records found among them. Mr. Adam's work in this department was interrupted by his being called up during the Great War, in which he made the Supreme Sacrifice.

Mr. W. E. Nicholson of Lewes, Sussex, an ex-president of the British Bryological Society, after reading the notes published in our *Transactions* asked for a list of wanted species, as did also Miss Armitage, another keen bryologist. They were kind enough to send several rare species, namely, *Catharinea angustata*, *Pottia commutata*, *Weisia Mittenii*, *Ephemerum intermedium*, and *Plagiothecium silesiacum*, all from East Sussex; *Webera calcarea* from Cornwall; and *Bryum cyclophyllum* from Cumberland. Mr. Nicholson sent a few other species of Continental origin of which he did not possess British specimens.

A good specimen of another rarity (*Tortula norvegica*) from

Craig Chailleach was presented by another member of the Society.

By the kind instrumentality of Mr. J. Rutherford Hill a very large collection of British and Foreign Mosses formed by the late Mr. William Smith, Arbroath, was presented by his widow. It contained about 4000 British specimens. Among them were found 80 new vice-county records and the following six species new to the Herbarium: *Catharinea tenella* from Tentsmuir, Fife; *Fissidens rivularis* from Sussex; *Tortula suberecta* from Angus; *Trichostomum inclinatum* from Fife and Angus; *Orthotrichum Schimperi* from South Devon; and *Webera gracilis* from Inverness.

A small but interesting collection mounted in book-form was presented by Mr. James Crichton Browne of Crindau, Dumfries. In his covering letter to Professor Sir William Wright Smith he said that the specimens had been gathered mainly by James Cruickshanks, his father's coachman, and a self-educated man. They had been collected chiefly in the counties of Angus and Dumfries during the years from 1832 to 1841. They had been dried, mounted, and named with great care and arranged in the order of the handbooks then in use.

Two volumes of Thomas Drummond's "Mosses of Scotland," published in 1824, were also received. They contained specimens of several very rare mosses, though none were new to the Herbarium, but still very welcome additions to it.

Lastly, a large collection consisting of about 5000 specimens was acquired from the widow of Mr. Robert H. Meldrum, Perth. They represented the labours of half a century. The majority had been collected by Meldrum himself principally in the counties of Perth and Angus. The remainder are from all parts of the British Isles. Both Meldrum and Smith maintained a large correspondence with other British botanists, consequently their Herbaria were very rich in rare species authenticated by specialists in this branch of botanical study. Meldrum's collection contained a number of interesting specimens more than a century old. There were some from R. Maughan (1805), W. J. Hooker (1808), George Don (undated), Greville (1820), Drummond (1824), besides a few of later date, as Nowell (1860), Wilson (1863), and Buchanan White (1864).

It was very gratifying to find in this collection of Meldrum's nine species of which there were no specimens in the Herbarium. They are as follow: *Fissidens algarvicus* from Glos; *Grimmia crinita* from Warwicks; *Barbula cordata* from Devon; *Fontinalis dolosa* and *F. dalecarlica* from Beds and Lancs respectively; *Leskea nervosa*, *Pseudoleskea striata* var. *saxicola*, *Plagiothecium piliferum*, and *Hypnum revolutum*, all from Ben Lawers. These are all exceedingly rare mosses, and they form a valuable addition to the Herbarium.

In August 1933 Mr. H. B. Gilliland, a former student at the University, visited the county of Moray and gathered over a hundred mosses. Of these ten were new records for that county, specimens of which he presented to the Herbarium.

In my previous note I stated that thirty-six species were unrepresented in the Herbarium. There are now only thirteen desiderata, namely, *Cynodontium gracilescens*, found once in Clova in 1868 but not seen since. *Trematodon ambiguus*, of which a single tuft was found by Dr. Braithwaite in 1883 at the base of Schiehallion, the sole record for Britain. *Grimmia Muehlenbeckii*, gathered in five counties only—two on the south coast of England and three in central Scotland. *Grimmia homodictyon*, once gathered by Mr. H. N. Dixon in 1899 in Sutherland. *Barbula glauca*, recorded from Sussex and Yorkshire. *Trichostomum limosellum*, once gathered by Dr. Stirton at Arisaig. *Orthotrichum pallens*, occurring in several counties from Cornwall to Aberdeen, and also in Ireland; it is probably overlooked because of its close similarity to a common species, *O. stramineum*. *Ephemerum stellatum*, the smallest British moss, occurring in Sussex and Kent. *Bryum Lawersianum*, discovered by Mr. Dixon in 1899, and again by Miss C. A. Cooper in 1924 on Ben Lawers. *Bryum rufifolium*, found in Denbigh and in West Ross. *Bryum Dixoni*, found by Mr. Dixon in 1898 in Argyll. *Heterocladium Macounii*, recorded from the Grampians and East and West Ireland. *Eurhynchium strigosum*, found by Tozer in Cornwall—the specimens are in the Hooker Herbarium; after many years it was found by the late Rev. J. Ferguson of Brechin in a single locality in Scotland.

Of the twenty-three species which have been added to the Herbarium since 1932, as showing their rarity, it is interesting

to note that nine of them have been found in only one locality, and of these five were growing on Ben Lawers. Eight others have been found in only two localities. With the exception of two they are from the most southerly counties of England —Devon and Sussex. In the latter county Mr. W. E. Nicholson has made many notable discoveries—proof of what can be done by careful and systematic examination. Many reputed rarities so very closely resemble common species of the same genus that very probably they have been overlooked. Accurate knowledge of the slight differences and the gift of distinguishing them in the field with a pocket lens are indispensable to the botanist who wishes to add to the records of the distribution of mosses.

There is still plenty of scope for enthusiastic students of this class of plants. The records for several counties in the North of Scotland are very meagre, particularly those bordering on the Moray Firth, and especially the uplands of the same. Many of the islands of the Hebrides and Shetland have hitherto been very imperfectly examined for both mosses and hepatics, and would yield abundant results to a keen qualified botanist.

An Inverted Willow Cutting (*Salix alba*). By R. J. D. Graham, H. Kate H. Hawkins, and the late L. B. Stewart. (With Pl. X.)

(Read 14th June 1934.)

A ten-year-old willow tree in which the lowest part, measuring 36 inches from the ground, was a cutting planted upside down is the subject of this paper. Planted in 1923, fig. 1 shows the plant in February 1925 with two strong leaders growing at the top of the inverted portion. All the buds which developed below the level of the lower branch were rubbed out in order to secure the development and continued growth of shoots as far from the ground as possible. In July 1926 (fig. 2) the lower branch had asserted control, which was maintained till the end of the experiment in May 1934 (figs. 3 and 4). It is obvious in all the figures that the inverted portion between the two shoots is distorted. This region was injured by rubbing against a support in the first year. The injury reached the cambium and the wood was exposed, though it was gradually being occluded.

Transverse cuts were made of the two leading shoots, E, the terminal small shoot, D, the lateral but larger leading shoot. The inverted portion was cut at C just below the injured zone and at B above ground level. The main root was cut 6 inches below ground level at A. Measurements of the growth attained each year were made at each annual ring, and the yearly diameters in millimetres are tabulated on next page.

It will be noted that the annual increase at B and C prior to inversion averaged 1·7 and 1·75 mm. respectively. In the ten completed years after inversion, *i.e.* to 1933, B averaged 5·9, C 4·6, D 5·9, E 2·1 mm. The largest annual increments are 7·25 mm. in the root, A, in 1924, and 11·5 and 5·25 in D and E in 1925. It is interesting to note that the maximum increment in the root antedates by one year the maxima in the shoots. It is important to note also that increments in B, the inverted portion, catch up with those in D from 1929, from which time the inverted portion increases more rapidly than the leading shoots. It is also of interest to note that a

	A.	B.	C.	D.	E.	Remarks.
Pith	..	2·5	3·5	2·25	3·5	Diameter in mm.
	..	1·25	2	..	..	"
	..	3·5	3·75	..	..	Before inversion
	..	5·75	6·5	..	..	Before inversion
	..	6·75	7	..	..	Before inversion
1924	3·75	9·35	12	1	1	
1925	11	12·25	16	8·5	3·75	Fig. 1, February
1926	15·75	16	19	20	9	Fig. 2, July
1927	18·5	18	23	27·75	12	
1928	23·25	23	29	34	14·5	
1929	28	28	32·5	38·75	17	
1930	33·5	35·25	35·75	41	18·75	
1931	37	44	43	47·75	19·25	
1932	42	52	49·5	54·5	20·25	
1933	47·5	66	53	57·5	21·25	
1934	53·5	67·5	53·25	58	22·25	Figs. 3 and 4, May

terminal root 53 mm. in diameter was regenerated on the cutting.

References to plants and plant portions grown upside down can be traced back to classical authors (1). The most important recent reference is by Vöchting (2), who figures a two-year-old inverted willow cutting. Vöchting records that the inverted portion of his willow failed to grow in thickness, and gradually died back. This was to be expected when the strongest shoot in his plant was just above ground level. In the present case growth in thickness of the inverted portion was exceeded by the leading shoot from 1924 to 1929, after which the inverted portion went ahead. A point which requires further investigation is to decide whether this initial inhibition in secondary growth is due to inversion of the stem, or simply the result of a smaller leaf area demanding less water-conducting tissue. Once the leaf area of the plant increases, the development of water-conducting tissue in the inverted portion increases with the demand.

The first authors have associated the name of the late L. B. Stewart with this paper as a tribute of affectionate regard and esteem.

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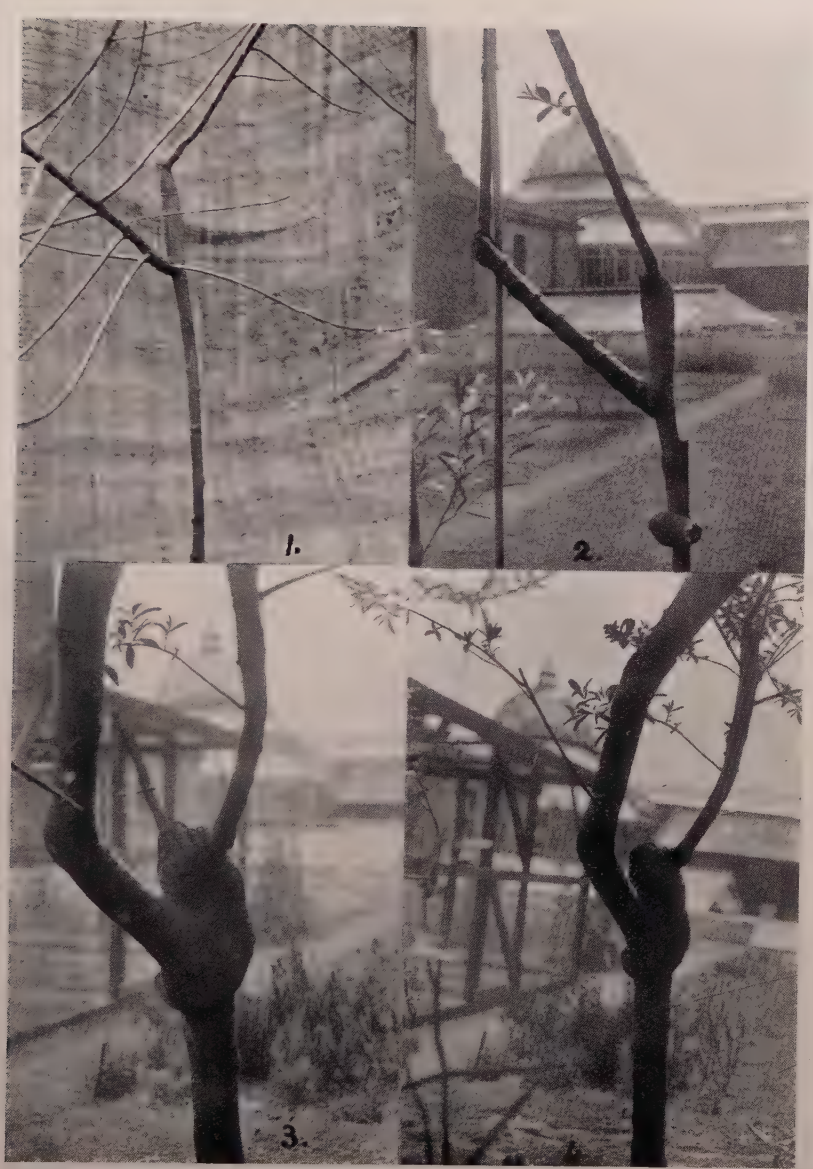

HAM, HAWKINS, and STEWART.

The Distribution of the Uredineae in Scotland.

By Malcolm Wilson, D.Sc.

(Read 14th June 1934.)

There are few if any countries besides Scotland in which an attempt has been made to give an account of the distribution of the whole of the fungi; that such an account appeared as early as 1879 is undoubtedly due to the fact that Scotland was particularly fortunate in possessing during the nineteenth century several individuals who, in addition to being noted mycologists, were enthusiastic naturalists of the type now almost extinct.

Rev. John Stevenson published his Mycologia Scotica in 1879, and in his preface he points out that R. K. Greville was the first in this country to give the study of Mycology a prominent place in literature by the publication of his Scottish Cryptogamic Flora in 1823–28, and that, following Greville, the Rev. M. J. Berkeley was the moving spirit of mycological study in Scotland.

It was especially the work of Greville and Berkeley that made the publication of the Mycologia Scotica possible, but many other investigators contributed. Subsequently to the appearance of the Mycologia Scotica, Stevenson published various additions and thus continued his work to 1886 (the later contributions being made in conjunction with Trail). From 1887–90 revisions of several of the larger groups of fungi were issued by Trail, and in these the distribution of the species in the various areas adopted by Stevenson was continued.

The Revision of the Uredineae and the Ustilagineae of Scotland, which appeared in 1890, was the last of this series. Since 1890 work on the distribution of Scottish fungi has been continued by members of the Scottish Cryptogamic Society, and in the Reports of the Annual Conferences, which, with the exception of the years during the War and 1922, have appeared regularly, all new records of species in the various areas have been noted up to 1924.

Thus, although many records of the occurrence of rusts have appeared since, Trail's "Revision" of 1890 (Scot. Nat., n.s. iv, pp. 302, 367) is the last account of the distribution of the group as a whole which we possess. It is in consequence taken as the basis of the present account.

An account of the literature dealing with the distribution of the Scottish fungi previously to 1879 is given by Stevenson.

One of the earliest lists appears to be that given by Thomas Hobkirk in the Flora Glottiana, published in 1813, which deals with plants found in the Clyde area; it contains an interesting account of the occurrence of *Gymnosporangium Sabinae*.

The importance of the work of R. K. Greville has been referred to already. A critical examination of the Scottish Cryptogamic Flora (1823–28) and the Flora Edinensis (1824) has supplied a few records not included by Trail. There is an interleaved copy of the Flora Edinensis in the library of the Royal Botanic Garden, Edinburgh, which appears to have been Greville's working copy, for in it a number of additional species are recorded in his handwriting; this has yielded a few records of the Uredineae, notably the occurrence of *Endophyllum Sempervivi* near Edinburgh. Greville's Herbarium is preserved at the Royal Botanic Garden, Edinburgh; according to Britten and Boulger's Biographical Index part is at Glasgow University, but inquiry has shown that no fungal specimens are now present there. The herbarium contains not only specimens collected by Greville, but also some from Carmichael of Appin. A number of records unknown to Trail have been discovered by an examination of this herbarium. The Flora Scotica of W. J. Hooker contains a short list of rust fungi, and although this appeared in 1821, a few years before the Flora Edinensis, the descriptions are very largely based on Greville's work.

Johnston lists a number of Uredineae in the Flora of Berwick, vol. ii, published in 1831, and this, together with his herbarium, which is preserved at the museum in Berwick, has supplied a number of new records.

The Flora of Forfarshire by William Gardiner appeared in 1848 and contains a list of fungi. Some of Gardiner's specimens of Uredineae are in the Edinburgh Herbarium and a larger number are preserved at the Dundee Museum.

The importance of the work of Berkeley has already been

referred to, and the accounts of the Uredineae in the English Flora (1836), the Outlines of Fungology (1860), and the Notices of British Fungi have been freely consulted.

Dickie's Botanist's Guide to the Counties of Aberdeen, Banff, and Kincardine, published in 1860, also contains a list of fungi, including a number of Uredineae.

In 1863 Jerdon published (in Hist. Berw. Nat. Club, 1863) a list of fungi found in the neighbourhood of Jedburgh, and a few specimens collected by this investigator are found in the Edinburgh Herbarium.

Collections of fungi were made by M. L. Anderson and J. Fergusson particularly from Angus, by Keith in the vicinity of Forres, and by Buchanan White from Perthshire; specimens of the Uredineae collected by these investigators are found scattered through the Kew, Edinburgh, and Trail Herbaria.

Between the appearance of Stevenson's Mycologia Scotica and Trail's Revision, Plowright's Monograph of the British Uredineae and Ustilagineae was published in 1889, and although this was a most important addition to the literature, it added very few additional Scottish records.

Trail's Revision showed a great advance on the list of Uredineae given by Stevenson; it not only contains a large number of new records, but, owing to the greatly increased knowledge of the group in the interval between the two publications, various rusts regarded by Stevenson as distinct were now placed in their true position as stages in the life-history of other species. Trail was a most assiduous collector, and the great majority of the new records were his own discoveries. His herbarium is kept at Aberdeen University, and in it there are two distinct collections of rust fungi; in one of these the specimens are arranged according to the host plants, other micro-fungi also being included; in the other only Uredineae are found, and these are arranged according to the system of Schröter as adopted by Plowright, which depends on the number of spore forms present in the species. In addition to these two collections a few rusts were found in a large collection of unclassified specimens, in many of which only the name of the host plant was given.

During the latter part of his life Trail was engaged on work on the distribution of the Scottish fungi, and a considerable number of outline maps showing the distribution of species

are kept at Aberdeen. He only published a few notes on the Uredineae after his "Revision."

Subsequent to Trail, D. A. Boyd was one of the most important contributors to the literature of fungal distribution in Scotland. His publications, which extended from 1892 to 1928, dealt for the most part with distribution in the Clyde area, but until 1924 he kept up to date the new records for species for the whole of the Scottish districts, these being published in the annual reports of the Scottish Cryptogamic Society. He published numerous articles in the Scottish Naturalist and elsewhere in which he described the occurrence of many new and interesting species.

On the occasion of the visit of the British Association to Glasgow in 1901 an account of the Fauna, Flora, and Geology of the Clyde Area was published, and in this Boyd was responsible for the list of fungi, in which a large number of Uredineae were included; in this several references are made to specimens in the Hennedy Herbarium, but it appears that these are no longer in existence.

In 1908 Lorrain Smith published a list of fungi from Dumfriesshire (Trans. Dumfs. Nat. Hist. Soc., n.s., xx, p. 170), and in this a number of rust fungi was included. Three important lists of British Uredineae appeared in 1913: "The British Rust Fungi," by W. B. Grove; a "List of the British Uredinales," by J. Ramsbottom (Trans. Brit. Mycol. Soc., iv, p. 77); and "Mildews, Rusts and Smuts," by G. Massee, but these recorded only few additions to the Scottish rusts. Since 1913 notes on the occurrence of Scottish rust fungi have been published by W. B. Grove, A. W. Borthwick, the author, and others.

In discussing the distribution of any group of living organisms some method of grouping records into areas must be adopted; the method by which such areas are delimited may be based on artificial (political) boundaries or on the natural configuration of the country. In works dealing with the distribution of the flowering plants comital boundaries have generally been chosen, and these are for the most part artificial. Although this method is convenient, the presence or absence of a species from such an area does not necessarily have any biological significance. Where the records are comparatively few, as in the case of rust fungi, it is convenient to choose

larger areas, and the value of the records is greatly increased if these are natural areas.

The areas adopted by Stevenson and used by Trail were those suggested by Buchanan White in his Catalogue of the Insects of Scotland (Scot. Nat., i). They are based on the drainage of the country and are as follows:—

Eastern Districts.

1. *Tweed.*—The part drained by the Tweed and other rivers entering the sea between Berwick and Cockburnspath.
2. *Forth.*—The part drained by the Forth and other rivers between Cockburnspath and Fife Ness.
3. *Tay.*—The part drained by the Tay and other rivers between Fife Ness and Cratown.
4. *Dee.*—The part drained by the Dee and other rivers between Cratown and Pitsligo.
5. *Moray.*—The part drained by rivers between Pitsligo and Ord of Caithness, and by the Caledonian Canal as far west as Loch Oich.
6. *Sutherland.*—The part drained by rivers between Ord of Caithness and Cape Wrath.
7. *Orkney.*
8. *Zetland.*

Western Districts.

1. *Solway.*—The part drained by rivers between the Liddel and Culzean Castle.
2. *Clyde.*—The part drained by the Clyde and other rivers between Culzean Castle and Loch Awe: includes Arran and Islay.
3. *Argyle.*—The part drained by rivers between Lochs Awe and Aylort: includes Mull, Tiree, and adjacent islands.
4. *West Ross.*—The part drained by rivers between Loch Aylort and Cape Wrath: includes Skye.
5. *Hebrides.*

It is to be noted that these are natural areas limited by watersheds, and in consequence the complete absence of any organism from one or more of them will have some biological significance. These areas are also generally comparable, for every one (except the islands) contains highland and lowland,

sea coast and tracts of cultivated ground, forest and moorland.

When the present list is compared with that drawn up by Trail it will be found that extensive alterations have been made in both nomenclature and arrangement. The arrangement of Schröter, adopted by Trail, has been rejected on account of our lack of knowledge regarding the life-history of many species. The system adopted is that followed by the brothers Sydow in their Monograph and by Grove in the British Rust Fungi, in which the species are arranged according to their host plants. The nomenclature adopted is generally that given by the brothers Sydow in their Monograph.

The number of species given in Trail's list is 147, while 240 are now recorded. The increase is due to (1) the splitting of a number of the species given in Trail's list, e.g. *Puccinia Galii* is now represented by *P. punctata*, *P. difformis*, and *P. Asperulae-odoratae*; (2) the discovery of species new to Scotland; (3) the inclusion of certain species recorded previously to the publication of Trail's list but omitted from it.

On the other hand, there has been a reduction in the number due to (1) the combination of some regarded as separate species by Trail but now recognised as different stages of the same species; (2) the exclusion of certain species which are now known to be non-existent in Scotland or of which the records are ambiguous.

Certain species have been placed in the list, although the evidence for their inclusion as Scottish rusts is not altogether satisfactory; whenever this is the case it has been noted under the species in question and the reasons for its inclusion are given.

Although many additional records of Uredineae have been made since the publication of the Mycologia Scotica, in the majority of cases no general statement regarding the distribution of a species can be made. The investigation of the fungal flora of the districts in the North and West is still very incomplete, and although the flora of the other districts has been more fully examined there is little doubt that many inconspicuous species have been overlooked. The following statement from Stevenson's work still holds good:—

"No attempt has been made to determine the comparative frequency or rarity of species. Perhaps the best indication

of this at present is the number of districts recorded under each. Further investigation, however, will doubtless prove that species which have as yet been found only in one locality are not uncommonly distributed. It must be borne in mind also that, in many instances, plants which have been found in nearly all of the districts are by no means common, often infrequent and extremely local."

Any conclusions regarding distribution which may be referred to subsequently in the discussion must therefore be considered as purely provisional.

The records of the Uredineae given in Trail's Revision for Forth, Tay, and Dee may be regarded as moderately representative for these areas, while the number of those from Tweed, Moray, and Clyde were somewhat less satisfactory; few records were given for Orkney and Argyle, and very few for Ross and Solway, while Sutherland, Hebrides, and Shetland were entirely unrepresented. The number of records given by Trail for each of the respective areas is given in the first column of the table. In the present work a special endeavour has been made to obtain records for the areas which were less represented in Trail's Revision. The number of new records for each of the respective areas is given in the second column of the table.

The totals given in the third column do not agree with the totals obtained by adding columns one and two since, as already explained, in discussing the number of species, some

Districts.	Records by Trail.	New Records.	Total.
Tweed . . .	68	56	115
Forth . . .	83	77	151
Tay . . .	117	62	163
Dee . . .	106	45	141
Moray . . .	78	54	125
Sutherland . .	..	30	30
Orkney . . .	28	15	40
Solway . . .	9	101	106
Clyde . . .	65	87	148
Argyle . . .	38	42	72
Ross . . .	15	42	56
	607	611	1147

of the records given by Trail are duplicates or are ambiguous and are, in consequence, ignored.

It should be noted that at the time of Trail's Revision more investigation had probably been carried out in Tay and Dee than in the other areas, and this partly accounts for the high number of records from each of these areas. The number of new records in any area will obviously depend to a considerable extent upon the number already published by Trail, *e.g.* the large number of new records from Solway is largely due to the fact that very few were recorded from this area by Trail. The greatest number of records for an area in Trail's Revision, 117, is found in Tay, and this has been increased by about 39 per cent. to 163 in the present account, about 68 per cent. of the total Scottish species being represented; it is still the highest number in any area.

It is estimated that since the time of Trail's publication an approximately equal amount of investigation has been carried out in the Forth, Tay, and Clyde areas, so that the large number of Tay records cannot be explained by more intensive work in that area. It may be provisionally concluded that the greatest number of rust fungi does actually occur in this area. This may be accounted for by the fact that it is one of the largest areas and is centrally situated. The different types of vegetation are also probably more fully represented in this area than in the others, and hence the number of potential host species is probably greater.

The numbers from the Forth, Clyde, and Dee areas are roughly equal and may be provisionally accepted as indicating the actual distribution. Although the Moray area is probably the largest, the number of records is smaller, probably due to less intensive investigation. The numbers from Tweed and Solway might be expected to be approximately equal since these are comparable areas, but the actual records are greater from the former, probably due to the greater investigation in that area. Argyle is a smaller area and has been less investigated; owing to its position and configuration it is probable that the number here is actually less.

The small numbers from Ross and Sutherland are undoubtedly partly due to less investigation, but it is probable that the actual numbers are smaller in these areas owing to their more northerly position.

The same remarks apply even more strongly to Orkney, but here, in addition, isolation from the mainland will almost certainly decrease the number.

The distribution of the rust fungi is obviously limited by that of their hosts, but it does not by any means follow that the distribution of the rust and its host is similar, and in many species it is known that this is not the case.

Puccinia Vincae has only been recorded in one area in Scotland, although its host plants (*Vinca minor* and *V. major*) are commonly found over the whole country, while *Puccinia-strum Agrimoniae* has only been recorded from the extreme south, although its host (*Agrimonia Eupatoria*) extends to Sutherland; it is interesting that *P. Agrimoniae* is reported as common in England. The case of *Puccinia perplexans* is interesting, for although both its host plants (*Ranunculus acris* and *Alopecurus pratensis*) are native and abundant in Scotland and are commonly associated, only one record of this species has been made. It is impossible to explain the occurrence of such rare species until we possess much greater information regarding the biology of all the species concerned.

The problem of distribution of a parasite is much more difficult than that of a holophyte, for in the former case two organisms, the host and its parasite, are concerned. Any change in the external conditions will affect both organisms, and the complex relation which exists between parasite and host may be thereby considerably altered.

It is now generally recognised that, in the case of the Uredineae, the amount of infection varies directly as the vigour of the host. The experiments of Marshall Ward, Stakman, Mains, and others among whom Hiratsuka (Bot. Mag. Tokyo, xlvii, 1933, p. 710) is one of the most recent, have dealt with the effects of the nutrients of the host upon the development of the fungus, and have shown that those host plants which receive a complete and suitable culture solution become the most heavily infected.

In considering the area of distribution of any plant we may conclude that the most vigorous development will be found towards the centre, and that on approaching the outskirts of the area the plant will decrease both in vigour and number. It would, in consequence, be expected that the abundance of any rust species would be greater at the centre of the

distribution area of its host, would diminish in passing outwards, and that the parasite might be altogether absent on the outskirts.

The production of spores by the rust fungi is as a general rule abundant, and it appears unlikely that the rarity of any species is determined by lack of reproductive bodies. Recent investigations have shown that spores may be distributed for long distances by wind and still retain their viability. In a comparatively small area, such as Great Britain, where no decided barriers to distribution exist, it is improbable that the absence of native species from any district depends on the fact that spores have never been carried there. It would appear rather to be due to some unfavourable factor in the environment which inhibits the development of the species.

As already pointed out, owing to the obligate parasitism of the Uredineae the influence of external factors on the species can generally only be investigated in connection with their hosts. The literature on the relation of the rust fungus and its host is extensive; it has been catalogued by Zimmermann in 1925 (Centr. Bakt., II, lxv), and has recently been summarised by Arthur (The Plant Rusts, 1929).

The influence of temperature on spore germination and infection has been the subject of several investigations, that of Hiratsuka (*loc. cit.*) being one of the most recent. It has been shown that the optimum temperature varies for different species and also for the different spore forms of the same species, but it does not appear that these observations have been correlated with the distribution of the species concerned.

In this connection an interesting observation has been recently made by Lamb (Trans. Roy. Soc. Edin., lviii) on *Puccinia Prostii*. This species, which occurs as a native in Italy and southern France, has been recently imported into Scotland; it produces abundant teleutospores, but up to the present all attempts to make these germinate have failed, and it is suggested that these, when produced in the climate of Edinburgh, are incapable of germination.

Observations have also been made on the effect of different light intensity and varying moisture content of the atmosphere, but here again the bearing of the results obtained on the distribution of species has not been investigated.

The highly developed specialisation of parasitism which

exists in the Uredineae and the varying resistance of the different forms and varieties of the host plants must evidently play an important part in the distribution, but at present little or nothing is known of their influence.

Certain rust fungi such as *Puccinia Sonchi* and *Phragmidium Rubi* are stated to occur more commonly in the vicinity of the sea, although their host plants (*Sonchus* sp. and *Rubus fruticosus* respectively) have a wide distribution, both inland and by the sea. In the vicinity of the sea it is probable that the temperature is more equable, the moisture content of the air is higher, and traces of salt may be present both in the atmosphere and soil; these factors may affect both host and parasite and possibly the relationship between the two. They may favour the existence of special physiological forms of the fungi with different powers of infection; forms of the host plants which differ slightly both morphologically and physiologically from these found farther inland may occur, and these may have differing powers of resistance. It is known that plants growing by the sea have in some cases an abnormally high osmotic pressure of the cell sap and this may have an influence upon their susceptibility to infection. There are, no doubt, other factors concerned, but those mentioned will illustrate sufficiently the complexity of the problem.

Some indication of the influence of the physiological factors may be obtained by a consideration of the relative numbers of species found in England and Wales and in Scotland. The number occurring in Great Britain is approximately 297; while in England and Wales alone 266 are found, and in Scotland alone 240.

In this comparison, however, it must be remembered that the areas compared are not equal, England and Wales being about double the size of Scotland; also, as pointed out on p. 351, owing to our incomplete knowledge of the distribution of the species any conclusions must be regarded as provisional.

It is known that throughout the world there is in general a decrease in the number of Uredineae towards the north, but how far this depends on the lower temperature in the more northern regions has not been determined. It is noteworthy that the average July temperature of the south of England (about 62° F.) is approximately 6° F. higher than that of the north of Scotland (about 56° F.).

It must be remembered, however, that in passing from the south of England to the north of Scotland there is a decrease in the number of potential host species, and although this is not great it will lead to some diminution in the number of rust species.

In his recent work on the Uredineae Arthur has emphasised the importance of a consideration of the life-history of the rust species, and he distinguishes macrocyclic (long-cycle) forms in which the mycelium exists both in gametophytic and sporophytic phases from microcyclic (short-cycle) forms in which only the gametophytic phase is present. In his discussion of geographical distribution of the species he has brought forward evidence to show that there is a relative increase in the number of microcyclic forms towards the north, and also in the regions of high altitude. It would be expected therefore that in Scotland the proportion of microcyclic forms would be higher than in England, and this appears to be the case. The increased percentage of microcyclic species in Scotland is, however, only small, and in the present state of our knowledge of distribution it is doubtful whether it has any real significance. If, however, only the genus *Puccinia* is considered there is no doubt that the percentage of microcyclic species is higher in Scotland owing to the fact that in the latter country a number of alpine micro species are found which do not occur in England.

As far as can be ascertained the following species occur in Scotland but not in England:—

Uromyces Genistae-tinctoriae.
,, *Ari-virginici.*
Puccinia Le Monnieriana.
* ,, *Porteri.*
* ,, *Veronicarum.*
,, *caulincola.*
,, *Soldanellae.*
* ,, *Rhodiolae.*
* ,, *Saxifragae.*
* ,, *Oxyriae.*
,, *Polygoni-vivipari.*
* ,, *septentrionalis.*
,, *Ribis.*
* ,, *borealis.*
,, *longissima.*
Phragmidium fusiforme.
,, *Rubi-saxatilis.*
Chrysomyxa Rhododendri.
**Melampsora arctica.*
* ,, *alpina.*
* ,, *reticulatae.*
,, *vernalis.*
**Caeoma Saxifragae.*
Pucciniastrum Goodyerae.
Hyalopsora Aspidiotus.
Milesina Polystichi.
,, *murariae.*
Uredinopsis filicina.
Uredo Lynchii.
,, *glyceriae.*
Aecidium Ranunculacearum var. *Linguae.*

Those marked with an asterisk may be regarded as definitely alpine species. It is noteworthy that in only three species (*Puccinia Porteri*, *P. Veronicarum*, and *Melampsora reticulatae*) are the respective host plants absent from England. *Uromyces Ari-Virginici*, *Puccinia Soldanellae*, *Chrysomyxa Rhododendri*, and *Uredo Lynchii* are imported species occurring on foreign host plants. The presence of only one native species of *Uromyces* in the list is of interest; for about thirteen species of *Uromyces* occur in England which are not found in Scotland. These facts are in agreement with the findings of previous investigators, for the genus *Uromyces* is known to have a more southerly distribution than the genus *Puccinia*.

The signs and contractions employed are similar to those employed in Trail's Revision. The mark (!) denotes that the record is a personal one, *i.e.* if it follows the name of a district it denotes that the fungus has been seen growing there by the author; if it follows the name of the host plant it denotes that it has been found on the plant indicated.

The number of the species in the Revision is given immediately after the name; the name used in the Revision is given in brackets if it differs from the name now used. The number of the page on which the species is described in the British Rust Fungi, by W. B. Grove, is also given. The letters *p.p.* (standing for *pro parte*) denote that the name in the Revision covers more than one species as now understood; and that the "species" in the subjoined list corresponds only in part to the name put after it in brackets.

An asterisk is prefixed to the names of species added to the Scottish records since 1890; new records of host plants are indicated in the same way.

New district-records are in italics; those previously given in the Revision being in ordinary type. The locality of the new district-records is given in brackets after the district.

The various stages of the fungi are denoted below as follows: 0 is the spermogonium, I the aecidial stage, II the uredospore stage, III the teleutospore stage.

Detailed descriptions of the species are given only when these do not appear in the British Rust Fungi, by W. B. Grove. Stages which have not been found in Scotland are enclosed within square brackets.

The following herbaria have been consulted:—

The Royal Botanic Garden, Edinburgh (for Herb. Greville. and other specimens).

The Royal Botanic Gardens, Kew (Herb. Kew.).

The British Museum (Natural History).

Aberdeen University (for Herb. Trail.).

The Municipal Museum, Berwick (for Herb. Johnston.).

The Municipal Museum, Dundee.

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UROMYCES Link.

1. Uromyces Valerianae Fckl.

Trail, No. 8; Grove, p. 86.

Tweed! Forth! Tay! Dee, Moray! Orkney.

Solway! *Clyde*! (Arran), Argyle!

0, I, II, III on *Valeriana officinalis*!

2. * Uromyces Scrophulariae Fckl.

Grove, p. 87.

Tay.

Argyle! (Taynuilt and Inverliever).

0, I, III on * *Scrophularia nodosa*!

Omitted by Trail, but recorded by Stevenson (M.S., No. 1372) as *Aecidium Scrophulariae* DC.

This, according to Kursanov (J. Russian Bot. Soc., i, 1916, p. 1), possesses a repeating aecidium, *i.e.* infections with aecidiospores result in the production of aecidia.

2a. * Uromyces Limonii Lév.

Grove, p. 88.

Solway! (Auchencairn).

I, II, III on * *Statice Limonium*!

This was collected by H. D. Gordon in June 1934, and forms the only record for Scotland.

3. Uromyces Armeriae Lév.

Trail, No. 3 (*U. Limonii* DC.); Grove, p. 89.

Tweed! (Berwick), *Forth*! (Edinburgh and Gullane), *Tay* (Perth), Dee, *Sutherland*! (Tongue).

Solway! (Ballantrae), Clyde, *Argyle* (Ardkinglas).

I, II, III on leaves and flower peduncles of *Armeria maritima*! * *A. grandiflora*, * *A. leucocephala*!

This was previously united with *U. Limonii* Lév. which occurs on *Statice Limonium* (see No. 2*a*). There is a specimen in the Herb. Edin. collected by Greville, probably in 1822, labelled "*Uredo Statices* on *Statice*. Edinburgh Botanic Garden." *U. Armeriae* is now found in the Royal Botanic Garden on *Armeria leucocephala*, and as Greville's specimen is identical with this and appears to be on the same host species, it is probable that the rust with its host plant has existed in this same locality for over one hundred years.

The rust on *A. grandiflora* was found by Buchanan White in Perthshire. Generally only uredospores and teleutospores are found on *A. maritima*, but Trail records aecidia on this species in May and June, and they have been found at Gullane in May.

All the spore forms occur on *A. leucocephala*.

4. * Uromyces Trifolii Lév.

Grove, p. 90.

Moray ! (Beauly).

II, III on * *Trifolium pratense* !

The only Scottish record is the specimen collected by J. Fraser at Beauly.

5. * Uromyces Trifolii-repentis Liro.

Trail, No. 5 (*U. Trifolii* A. et S. p.p.); Grove, p. 91.

Tay (Blair Atholl).

Solway (Girvan), *Clyde* (West Kilbride).

0, I, II, III on * *Trifolium repens*.

The aecidial stage is rare, but is reported as *Aecidium trifoliorum* Cast. by Stevenson (M.S., No. 1378) from Menmuir and Clova. These are possibly the specimens referred to by Grove (p. 92).

6. * Uromyces flectens Lagh.

Grove, p. 92.

Forth ! (Edinburgh and Borthwick), *Tay* ! (Ballinluig), *Dee* (Aberdeen), *Moray* ! (Beauly), *Sutherland* ! (Durness).

Clyde (Balloch, Toward, West Kilbride), *Ross* ! (Skye).

III on * *Trifolium repens* !

Reported by Boyd from several localities in the Clyde area (Glasgow Nat., vii, 1913, p. 10, and viii, 1916, p. 4) and from Ballinluig by Wilson (Trans. Brit. Mycol. Soc., ix, 1924, p. 139). A specimen in the Herb. Trail. collected at Aberdeen in 1880 and labelled *U. apiculosa* belongs to this species.

6a. * Uromyces Jaapianus Kleb.

Krypt. Fl. Brandenb., v, 1913, p. 239.

Dee (St. Fergus and Old Machar).

Uredospores.—Sori amphigenous, without spots, scattered, occasionally aggregated and confluent, minute, pulverulent, cinnamon; spores globose to broadly ovate, epispore 2–3 μ

thick, sparsely echinulate with spines 2·5–3 μ distant, yellowish-brown, 20–25 × 20–23 μ, with 5–6 germ-pores.

Teleutospores.—Sori similar but darker in colour. Spores globose to obovate, pale brown, epispore 2–3 μ thick, echinulate with strong spines 2·5–3 μ distant, 19–22 × 16–20 μ, germ-pore covered with a flat cap, pedicels short.

II, III on * *Trifolium dubium* (*T. minus*).

This species was discovered in Aberdeenshire in 1920 by Alexander Smith and again found in 1926. Only uredospores were present.

7. * Uromyces Loti Blytt.

Grove, p. 94.

Tweed ! (Berwick).

[0, I on *Euphorbia Cyparissias.*]

II, III on * *Lotus corniculatus* !

The only record is the specimen bearing uredospores only, collected by M. Y. Orr at Berwick in 1922. The aecidia have not been found in Britain.

8. Uromyces Anthyllidis Schröt.

Trail, No. 11; Grove, p. 95.

Forth, Tay, Dee, Moray, *Sutherland* ! (Durness), Orkney.

II, III on *Anthyllis Vulneraria* !

9. Uromyces Ervi Westendorp.

Trail, No. 16; Grove, p. 96.

Tay, *Orkney.*

Clyde.

I, II, III on *Vicia hirsuta.*

The Orkney record is by G. Sutherland; the Clyde record is from the British Association list of Fungi of the Clyde area.

10. Uromyces Fabae De Bary.

Trail, No. 1; Grove, p. 97.

Tweed, Forth! Tay, Dee, Moray.

Solway ! (Dumfries), Clyde, Argyle.

0, I, II, III on *Vicia Cracca, V. sepium* ! *V. sativa, Faba vulgaris* ! and *Lathyrus pratensis.*

Collected at Dumfries by Miss I. Maxwell. The record on *Lathyrus pratensis* by Trail may possibly be an error as the rust on this host in the Herb. Trail. is *Uromyces Pisi* (*q.v.*, No. 12).

11. Uromyces Orobi Lév.

Trail, No. 2; Grove, p. 99.

Tweed, Forth, Tay, Dee! Moray! *Sutherland*! (Tongue).

0, I, II, III on *Lathyrus macrorrhizus*!

12. * Uromyces Pisi Wint.

Grove, p. 99.

Tweed! (Cove), *Forth*! (Borthwick and Tynehead), *Tay*! (Brechin), *Dee* (Aberdeen).

Solway! (Drummore).

[I on *Euphorbia Cyparissias*.]

II, III on * *Lathyrus pratensis*!

This rust has not been previously recorded from Scotland. The aecidial stage, which occurs very rarely in England, has not been found, but uredospores are not uncommon on *Lathyrus pratensis*, and occasionally teleutospore sori are found on the lower parts of the stems; the infection is frequently very heavy, the lower leaves and stems being almost completely covered by the rust-coloured uredospores. There is a specimen collected near Edinburgh by Greville in 1822 in the Herb. Edin., and one in the Herb. Trail. collected at Aberdeen in 1882.

According to Grove (British Rust Fungi, p. 100) it is doubtful whether *U. Pisi* has been previously recorded on *Lathyrus pratensis* in Britain. When only uredospores are present there is difficulty in distinguishing this species from *U. Fabae*; in the former, however, the uredospores are finely verruculose, while in the latter they are distantly echinulate.

12a. * Uromyces Genistae-tinctoriae Wint.

Sydow, Monograph, ii, p. 90.

Moray! (Inverness).

Uredospores.—Sori hypophyllous, situated on pale spots, scattered or grouped and confluent, pulverulent, pale brown; spores globose, subglobose or ellipsoid, minutely echinulate, yellowish-brown, 20–28 × 18–24 μ, epispore 1·5–2 μ in thickness with 3–6 germ-pores.

Teleutospores.—Sori similar to the uredospore sori; spores globose, subglobose or ovate, with a minute hyaline papilla, pale brown, membrane of variable structure, verrucose or with the upper part verrucose and the lower part longitudinally

striate or striate all over, 16–28 × 14–20 μ; pedicels short, hyaline, deciduous.

II, III on * *Genista anglica*!

This was found by J. A. Macdonald in September 1934; only uredospores were present. This is the first record of the species for Great Britain.

13. Uromyces Geranii Otth. et Wart.

Trail, No. 6; Grove, p. 103.

Tweed, Forth! Tay! Dee! *Moray*! (Beauly).

Clyde.

0, I, II, III on *Geranium sylvaticum*! and *G. pratense*!

13a. Uromyces Kabatianus Bubák.

Grove, p. 104.

Forth! (Edinburgh).

0, I, II, III on **Geranium pyrenaicum*!

This rust was found in July 1934 and is a new record for Scotland. It is distinguished from *U. Geranii* (see No. 13) by its paler, longer teleutospores, more oblong in shape with a higher papilla, arranged in paler, generally more circinate, sori; these are only produced late in the autumn. The uredospores are similar to those of *U. Geranii* but are produced on yellow spots with usually more circinate sori.

14. Uromyces Alchemillae Pers.

Trail, No. 13; Grove, p. 106.

Tweed, Forth! Tay! Dee! *Moray*! Orkney.

Solway! (Lockerbie and Thornhill).

II, III on *Alchemilla vulgaris*!

15. Uromyces Ficariae Lév.

Trail, No. 17; Grove, p. 107.

Tweed, Forth! Tay! Dee, Moray!

Solway! (Castle Douglas), *Clyde*!

III on *Ranunculus Ficaria*!

16. * Uromyces caryophyllinus Wint.

Grove, p. 108.

Clyde (Finlaystone).

II, III on **Dianthus Caryophyllus* (cult).

Recorded by Boyd (Trans. Brit. Mycol. Soc., iii, pt. 2, 1909, p. 122, and Glasgow Nat., i, 1909, p. 110).

17. Uromyces Behenis Unger.

Trail, No. 14 and p. 367; Grove, p. 109.

Forth (Aberlady), Tay, Dee, *Orkney*.

Clyde, Ross! (Gairloch).

I, III on *Silene maritima* and * *S. inflata* var. *puberula*.

The specimen from Aberlady in the Herb. Edin., collected by R(obert) M(ackenzie) S(tark) in 1836 on *Silene inflata* var. *puberula*; aecidia only are present. The Orkney record is by G. K. Sutherland.

18. * Uromyces sparsus Lév.

Grove, p. 111.

Forth! (Longniddry).

II, III on * *Spergularia rubra*!

The only record for Scotland is the specimen collected at Longniddry by J. K. Leven (Trans. Brit. Mycol. Soc., xii, 1927, p. 114). It is very rare in England, but its occurrence has recently been described by Grove and Chesters (Trans. Brit. Mycol. Soc., xviii, 1934, p. 265).

19. * Uromyces Betae Lév.

Trail, No. 7; Grove, p. 113.

Dee (Aberdeen), *Moray* (Nairn).

0, I, II, III on * *Beta vulgaris*.

Both records are by Mrs. N. L. Alcock on cultivated beet.

20. Uromyces Rumicis Wint.

Trail, No. 12 (*Uromyces Rumicis* Schum. p.p.); Grove, p. 114.

Tweed! Forth, Tay! Dee, Moray, Orkney.

Solway, Clyde! Argyle, Ross.

II, III on *Rumex conglomeratus*, *R. crispus*! and *R. obtusifolius*!

21. * Uromyces Acetosae.

Trail, No. 12 (*Uromyces Rumicis* Schum. p.p.); Grove, p. 116.

Tay! (Ballinluig), *Dee*! (Lumphanan), *Moray*! (Aviemore), *Sutherland*! (Ben Loyal).

Solway! (Girvan), *Clyde*! (West Kilbride and Strachur), *Argyle*! (Inverliever), *Ross*! (Kintail and Skye).

0, I, II, III on * *Rumex Acetosa*!

The aecidial stage was collected by W. Evans on the Isle of May in May 1912, and was found at Inverliever, Argyleshire, in May 1923; it has recently been recorded from England by Grove and Chesters (Trans. Brit. Mycol. Soc., xviii, 1934, p. 269).

Rumex Acetosella is also given as a host in England, but there appears to be no record on this species in Scotland.

Puccinia Acetosae also occurs on this host, and where teleutospores are not present the two species may be confused. For distinctions see No. 108 (under *P. Acetosae*).

The aecidial stage of *Puccinia Trailii* which also occurs on this host may be distinguished by its larger aecidial sori (up to 1·5 cm. in diam.) which are hypophyllous, with white pseudoperidia and strikingly white spores; the sori of *U. Acetosae* are smaller (up to 1 cm. in diam.), amphigenous (in the Argyleshire specimen epiphyllous), or on the petiole, with distinctly yellowish pseudoperidium and spores.

22. Uromyces Polygoni-Avicularis Ramsb.

Trail, No. 4; Grove, p. 117.

Tweed, Forth! Tay! Dee, Moray.

Solway! (Ballantrae), Clyde.

0, I, II, III on *Polygonum Aviculare*! and its sub.-sp. *P. Roberti* Loisel.

23. Uromyces Scillarum Wint.

Trail, No. 18; Grove, p. 120.

Tweed! (Chirnside), *Forth*! (Edinburgh), Tay! Moray!

Solway! (Newton Stewart), Clyde!

III on *Scilla nutans*! and * *Muscari polyanthum*!

This species was found on *Muscari polyanthum*, a new host plant for Britain, in the Royal Botanic Garden, Edinburgh. (See Notes, R.B.G. Edin., viii, 1914, p. 220).

24. * Uromyces Ari-virginici Howe.

Sydow, Monograph Uredin., 2, p. 295.

Forth! (Edinburgh).

Spermogonia.—On a perennial mycelium, chiefly hypophyllous, scattered, honey coloured, becoming brownish.

Aecidia.—On a perennial mycelium, chiefly hypophyllous, scattered, hemispherical before dehiscence, at length cup-

shaped with colourless recurved peridium; spores subglobose or ellipsoid, 15–20 × 17–24 μ, pale yellow, finely verrucose.

[*Uredospores.*—Sori amphigenous, without or seated upon very small spots, scattered or sometimes in small groups, ·5–·8 mm. diam., surrounded by the ruptured epidermis, pulverulent, yellowish-brown; spores generally oblong or clavate, rarely ellipsoid, apex thickened (up to 9 μ), sparsely echinulate (principally at the apex), yellow 28–45 × 17–25 μ, epispore 3–3·5 μ thick with four equatorial germ-pores.

Teleutospores.—Sori similar, brown; spores ovate or oblong with a pale subhyaline apical papilla 7 μ high, smooth, yellow or yellowish-brown, 28–45 × 20–28 μ, epispore 2–2·5 μ thick, pedicels short, hyaline, deciduous.]

0, I, II, III on leaves of * *Peltandra virginica.*

The uredospores and teleutospores have not been recorded for Great Britain. *Aecidium importatum* P. Henn., which is regarded by Sydow (Monograph, iv, p. 358) and Arthur (North Amer. Flora, vii, Uredinales, p. 236) as the aecidial stage of this species, was recorded by Hennings from the Berlin Botanic Garden (Verhandl. Bot. Verein Provinz Brandenburg, xxxvii, 1895, pp. xxv and 12) and later from the Edinburgh Botanic Garden (Wilson and Waldie, Trans. Brit. Mycol. Soc., xii, 1927, p. 114). Neither in Berlin nor in Edinburgh is the aecidial stage followed by either of the other spore conditions. The aecidial mycelium is perennial in the rootstock and aecidia are produced year after year on the infected plants; apparently the fungus under these conditions does not cause any injury to the host plant. The aecidiospores of *Aecidium importatum* as described by Hennings and as found in Edinburgh are considerably larger (25–30 × 20–27 μ) than those of *U. Ari-virginici* (17–24 × 15–20 μ); this fact and the constant absence of uredospores and teleutospores from *Aecidium importatum* throws some doubt on its identity with *U. Ari-virginici.*

25. * Uromyces Airae-flexuosi Ferd. et Wge.

Tweed! (Peebles), *Forth*! (Edinburgh), *Tay* (Crieff and Dunkeld), *Moray*! (Beauly and Forres).

Solway (Moniaive), *Ross*! (Mallaig).

Uredospores.—Sori epiphyllous, between the nerves, at first forming conspicuous, orange-yellow spots on the under surface,

occasionally hypophyllous, scattered or arranged in short rows 3–1 mm. long, remaining covered by the epidermis for rather a long time, intensely yellow; uredospores almost spherical, oval or ellipsoidal, distantly verruculose, 20–27 × 18–22 μ, membrane hyaline, up to 3 mm. thick with 6–8 scattered germ-pores; paraphyses absent.

Teleutospores.—Sori dark brown, epiphyllous or hypophyllous; teleutospores oval, oblong or pear-shaped, smooth, bright yellowish-brown, 30–33 × 17–20 μ, membrane thickened slightly at base and apex and deeper coloured at the latter; pedicels hyaline, equal in length to the spore, rather thick, persistent.

II, III on **Aira flexuosa*!

This species has not been previously recorded in Scotland, but is referred to by Grove (p. 265) in a note under *Puccinia dispera*. It was for some time found only in the uredospore stage and was known as *Uredo Airae-flexuosa* Liro (Sydow, Monograph, iv, p. 600), but in 1920 teleutospores were discovered by Ferdinandsen and Winge in Denmark (Bull. Soc. Mycol. France, xxxvi, 1920, p. 162). It is widely distributed on *Aira flexuosa* in Scotland but almost always only in the uredospore condition, teleutospores having been found only once, near Peebles. On this host it produces bright yellow spots which extend round the whole of the under surface of the leaf, and as these are up to 5 mm. long and often numerous a very characteristic appearance is produced, the leaf showing alternate green and yellow bands; only the leaves are attacked.

26. * Uromyces Dactylidis Otth.

Grove, p. 125.

Tweed! (Cove and Chirnside), *Forth*! (Borthwick and Ratho), *Tay*! (Ballinluig).

Clyde! (Troon and Dalrymple).

0, I on **Ranunculus repens*!

II, III on **Dactylis glomerata*!

Omitted by Trail. The aecidial stage is morphologically indistinguishable from those of *Uromyces Poae*, *Puccinia perplexans*, and *P. Magnusiana*; the last, however, appears July and August, while that of *U. Dactylidis* is usually found from March to May (see Nos. 27, 146, and 147).

27. Uromyces Poae Raben.

Trail, No. 10; Grove, p. 127.
Tweed! Forth! Tay! Dee, Moray, *Orkney*.
Solway, Clyde.
0, I on *Ranunculus repens*! and *R. Ficaria*!
II, III on *Poa pratensis*! and *P. trivialis*!

PUCCINIA Pers.

28. Puccinia Tripolii Wallr.

Trail, No. 93 (*Puccinia Asteris* Duby); Grove, p. 129.
Forth! (Aberlady), Tay, Dee, *Moray* (Findhorn).
III on *Aster Tripolium*!

29. Puccinia Virgaureae Lib.

Trail, No. 75; Grove, p. 130.
Tay, Dee.
Ross! (Mallaig and Glen Shiel).
III on *Solidago Virgaurea*!

30. Puccinia Millefolii Fckl.

Trail, No. 94; Grove, p. 131.
Dee!
Solway! (New Galloway), *Clyde* (West Kilbride and Stevenston).
III on *Achillea Millefolium*!

31. * Puccinia Chrysanthemi Roze.

Grove, p. 131.
Tay (Dundee).
Clyde (Glasgow).
II, III on * *Chrysanthemum indicum* and * *C. sinense*.
This species has been found on cultivated Chrysanthemums in several localities.

32. * Puccinia Absinthii DC.

Trail, No. 61 (*Puccinia Tanaceti* DC. p.p.); Grove, p. 134.
Forth! (Elie and Kincraig).
II, III on * *Artemisia Absinthium*!
This species was recorded by Trail at Kincraig (Scot. Nat., 3rd ser., i, 1891, p. 31) but included under *P. Tanaceti* in his Revision. It was also collected by J. F. Jeffrey at Elie.

33. Puccinia Tanaceti DC.

Trail. No. 61 (*Puccinia Tanaceti* DC. p.p.); Grove, p. 135.

Tay (Cherleton).

II, III on *Tanacetum vulgare.*

Collected by Rev. J. Ferguson (Scot. Nat., 3rd ser., i, 1891, p. 31).

34. Puccinia expansa Link.

Trail, No. 84 (*Puccinia Senecionis* Lib.); Grove, p. 136.

Forth! (Edinburgh and Dunbar), Tay! Dee, *Moray*! (Beauly), *Sutherland*! (Cape Wrath), Orkney.

Solway! (Thornhill and Lockerbie), *Clyde* (West Kilbride), *Argyle*! (Taynuilt), *Ross*! (Mallaig).

III on *Senecio Jacobaea*! and *S. aquaticus*!

35. Puccinia glomerata Grev.

Trail, No. 85; Grove, p. 136.

Tweed! Forth! Tay, Dee, Moray!

Solway (Girvan), *Clyde* (Milngavie), *Argyle* (Inveraray).

III on *Senecio Jacobaea*!

36. Puccinia Centaureae DC.

Trail, No. 58; Grove, p. 139.

Tweed! Forth! Tay! Dee, Moray.

Solway! (Ballantrae and Lockerbie), Clyde! Argyle, *Ross*! (Skye).

II, III on *Centaurea nigra*!

37. * Puccinia Carduorum Jacky.

Trail, No. 56 (*Puccinia Hieracii* Schum. p.p.); Grove, p. 141.

Forth! (Dalmeny), *Dee*! (Durris).

II, III on * *Carduus crispus*!

38. * Puccinia Cardui-pycnocephali Syd.

Grove, p. 142.

Tweed! (Cockburnspath), *Forth*! (Dunbar).

II, III on * *Carduus pycnocephalus*!

This species, which has only been previously recorded from the south coast of England, was found in several localities on the south-east coast during 1930.

P. galatica Syd. was previously separated from this species on account of its amphigenous sori with smaller, darker-

coloured, thick-walled, and delicately punctate teleutospores, but the two species are now combined (Sydow, Monograph, i, pp. 34 and 852).

In the Scottish specimens the sori are amphigenous.

39. * Puccinia Cirsii Lasch.

Stevenson, No. 1318 (*Trichobasis Cirsii* Lasch), Grove, p. 142.

Tweed! (St. Mary's Loch, Innerleithen), *Forth*! (Dunblane), *Tay*! (Dunkeld), *Dee*, *Moray*! (Inverness, Forres, Aviemore), *Sutherland*! (Ben Loyal).

Solway! (Thornhill, Ballantrae), *Clyde* (West Kilbride), *Argyle*! (Taynuilt).

II, III on * *Cnicus palustris* and * *Carduus heterophyllus*.

Although this species is included by Stevenson it is omitted by Trail. It is widely distributed on *Cnicus palustris*, but more uncommon on *Carduus heterophyllus*. A specimen on the latter host collected by Keith in August 1878 at Rothiemurchus was found in the Herb. Trail., and a similar specimen collected by Greville at Forres is in the Herb. Edin. It has also been found on this host near Inverness and at Dunkeld (Trans. Brit. Mycol. Soc., ix, 1924, p. 135). *Puccinia Andersoni*, which also occurs on *C. heterophyllus*, is distinguished by the absence of uredospores, its hypophyllous sori, and the distinctly thickened apex of the teleutospore.

The record of *P. Cirsii* on *Cnicus lanceolatus* at Dunkeld (Scot. Crypt. Soc. Rpt., 1925) probably refers to *P. Cirsii-lanceolati* Schröt. (*q.v.*, No. 40).

40. * Puccinia Cirsii-lanceolati Schröt.

Trail, No. 56 (*Puccinia Hieracii* Schum. p.p.); Grove, p. 143.

Forth! (Gullane and Dunfermline), *Dee* (Aberdeen and Forfar), *Moray*! (Aviemore and Cullen), *Sutherland*! (Durness), *Orkney* (Burray).

Solway! (New Galloway), *Clyde*! (Arran), *Ross*! (Skye).

Aecidiospores.—Aecidia hypophyllous, seated on minute, yellow spots, mostly solitary, at first closed and then opening by a circular pore, at length widely cup-like, scarcely provided with a proper wall, white; spores globose or ellipsoid, verruculose orange-yellow, 22–35 × 20–28 μ, with rather thick epispore.

Uredospores.—Sori mostly epiphyllous, scattered or often grouped and confluent, surrounded by the ruptured epidermis, pulverulent, ferruginous; spores globose or ovate, echinulate, brown, 24–36 × 20–26 μ.

Teleutospores.—Sori mostly epiphyllous scattered or grouped, minute, surrounded by the ruptured epidermis, pulverulent, dark brown; spores ellipsoid with unthickened rounded apex, not or scarcely constricted, base rounded or slightly attenuate, punctate, pale brown, 30–40 × 22–25 μ; pedicels short hyaline.

I, II, III on **Cnicus lanceolatus*!

This species is widely distributed in Scotland and has been described from several localities in England. The aecidial stage has recently been discovered both in Scotland and England (Grove and Chesters, Trans. Brit. Mycol. Soc., xviii, 1934, p. 271).

41. * Puccinia Le Monnieriana Maire.

Solway! (Drumlanrig), *Clyde*! (Arran).

Teleutospores.—Sori hypophyllous, seated on slightly depressed yellowish spots about 2–4 mm. in diameter, in small, irregular dense groups about 2–3 mm. wide, often confluent, pulvinate, surrounded by the ruptured epidermis, dark brown; spores clavate, apex rounded, truncate or acutely conical, strongly thickened (8–14 μ), constricted at the septum, rounded or often attenuate at the base, smooth, yellowish-brown, 40–55 × 14–21 μ; pedicels hyaline or brownish near the apex, thick (6–8 μ), persistent, up to 65 μ long.

III on * *Cnicus palustris*!

The species was first found by Maire in France, and the Scottish specimens have been confirmed by him. The species differs from all others found on the genus *Cnicus* by the very strongly thickened wall found at the apex of the spore, being most nearly approached in this character by *P. Cnici-oleracei.*

It is distinguished from this species by the smaller, often confluent sori and by the more strongly thickened, often pointed teleutospores. The species was first recorded from Drumlanrig in 1924 (see Wilson and Waldie, Trans. Brit. Mycol. Soc., xii, 1927, p. 113) and this was the first record from Britain.

42. Puccinia Cnici-oleracei Pers.

Trail, No. 95 (*Puccinia Cardui* Plowr.); Grove, p. 144.

Tweed, Forth, Tay, Dee, Moray.

Clyde (Ayr).

III on *Cnicus lanceolatus*!, *C. palustris*, and *Carduus crispus*.

Recorded on *C. palustris* by Boyd from Ayrshire and Arran (Glasgow Nat., viii, 1916, p. 55).

The records on *Carduus crispus* by Plowright (p. 216) and Trail are doubtful.

43. Puccinia obtegens Tul.

Trail, No. 54 (*Puccinia suaveolens* Pers.); Grove, p. 145.

Tweed, Forth! Tay! Dee, Moray, *Orkney*.

Solway! (Sandhead), Clyde, Argyle.

0, II, III on *Cnicus arvensis*!

44. Puccinia Andersoni B. et Br.

Trail, No. 76; Grove, p. 146.

Tay! Dee, Moray!

Argyle! (Taynuilt).

III on *Carduus heterophyllus*!

45. Puccinia Lapsanae Fckl.

Trail, No. 24; Grove, p. 147.

Tweed! (Berwick), Forth! Tay! Dee, Moray! *Orkney*.

Solway (Lockerbie), *Clyde* (West Kilbride), Argyle!

0, I, II, III on *Lapsana communis*!

46. * Puccinia Hypochaeridis Oud.

Forth! (Edinburgh), *Tay*! (Ballinluig), *Dee* (St. Fergus), *Moray* (Cullen).

Solway! (Lockerbie and Ballantrae), *Clyde*! (Arran), *Argyle*! (Taynuilt and Cladich), *Ross*! (Mallaig).

II, III on **Hypochaeris radicata*!

Omitted by Trail from his list, but apparently recorded by him as *Puccinia Hieracii* at Cladich (Scot. Nat., iv, p. 59). Grove states that only uredospores have been found in British specimens, but teleutospores were found in Edinburgh, Aberdeenshire and Banffshire among the primary uredospores in June.

47. * Puccinia Leontodontis Jacky.

Trail, No. 56 (*Puccinia Hieracii* Schum. p.p.); Grove, p. 149.

Forth! (Pittenweem), *Tay* (Barry), *Dee* (Aberdeen), *Moray*! (Aviemore).

Solway! (Ballantrae), *Clyde* (West Kilbride).

II, III on *Leontodon autumnalis*!

48. Puccinia Tragopogi Corda.

Trail, No. 68; Grove, p. 150.

Tweed! *Forth*! (Edinburgh), Tay.

0, I, II, III on *Tragopogon pratense*!

49. * Puccinia Prenanthis Auct. p.p.

Grove, p. 151 (*Puccinia Chondrillae* Corda).

Forth (Balmuto), *Tay* (Angus), *Moray*! (Beauly).

I, II, III on * *Lactuca muralis*!

50. Puccinia variabilis Grev.

Trail, No. 25; Grove, p. 152.

Tweed! Forth! Tay! Dee, Moray! *Sutherland*! (Tongue), *Orkney*.

Solway (Moffat), Clyde!

I, II, III on *Taraxacum officinale*!

51. Puccinia Taraxaci Plowr.

Trail, No. 59; Grove, p. 154.

Tweed (Berwick), Tay, Dee, Moray! Orkney.

Clyde! Argyle!

0, II, III on *Taraxacum officinale*!

52. Puccinia Sonchi Rob.

Trail, No. 66, No. 143 (*Aecidium Sonchi* Johnst.), and p. 367; Grove, p. 155.

Tweed! *Forth*! (Edinburgh and North Berwick), Tay, Dee, *Moray*! (Beauly).

Solway! (Stranraer), *Clyde*! (Arran and West Kilbride), *Argyle*! (Oban), *Ross*! (Kintail).

0, II, III on *Sonchus asper*! *S. arvensis*! *S. oleraceus*!

Teleutospores have been found in England near Hull in 1922 (Trans. Brit. Mycol. Soc., ix, 1924, p. 136) and in Aberdeenshire. Many mesospores are often present.

53. * Puccinia Crepidis Schröt.

Grove, p. 156.

Tweed! (Kelso), *Tay*! (Ballinluig), *Moray*.

Clyde! (Arran).

0, I, II, III on **Crepis virens*!

Recorded by Keith from Moray (Scot. Nat., 1884, p. 270) and by the author from Ballinluig in 1915 (Journ. Bot., lvii, 1919, p. 163). Usually only uredospores are present; the aecidium has not been found in Britain.

54. * Puccinia major Dietel.

Trail, No. 24 (*Puccinia Lapsanae* Schultz, p.p.); Grove, p. 157.

Tweed! (Peebles), *Forth*! (Balmuto and Ben Ledi), *Dee* (Braemar), *Moray* (Forres and Dulsie), *Sutherland*! (Tongue).

Solway! (Moffat), *Clyde*! (Arrochar and Strachur), *Argyle*! (Taynuilt), *Ross*! (Mallaig).

0, I, II, III on **Crepis paludosa*!

There is a specimen of this species in the Herb. Edin., collected by Greville at Balmuto, Fife, labelled *Aecidium Prenanthis*. It was collected at Forres by Keith in 1883 and the specimen is preserved in the Herb. Trail. (as *Puccinia flosculorum* A. et S. (Scot. Nat., i, 1883–4, p. 270), and also by Trail at Braemar in 1882 (as *Puccinia Lapsanae* Schultz, Scot. Nat., iv, 1877–8, p. 59). It is not uncommon in Scotland.

55. Puccinia Hieracii Mart.

Trail, No. 56 (*Puccinia Hieracii* Schum. p.p.); Grove, p. 158.

Tweed (Berwick), *Forth*! (Burntisland), *Tay*! (Ballinluig), *Dee* (Nigg), *Moray*! (Beauly), *Sutherland*! (Ben Loyal).

Clyde (West Kilbride).

0, II, III on *Hieracium Pilosella*! *H. alpinum*! *H. murorum*! *H. vulgatum*!

56. Puccinia Campanulae Carm.

Trail, No. 70; Grove, p. 159.

Tay! Dee.

Clyde (West Kilbride), Argyle.

III on *Campanula rotundifolia*!

57. Puccinia Adoxae Hedw.

Trail, No. 82; Grove, p. 160.

Tweed (Jedburgh), Forth! Tay! Dee, Moray!

Solway! (Sanquhar), *Clyde*.

III on *Adoxa Moschatellina*!

58. Puccinia albescens Plowr.

Trail, No. 28; Grove, p. 162.

Tweed, Forth, Tay, Moray!

Solway (Sanquhar), *Clyde* (West Kilbride and Garscube).

0, I, II, III on *Adoxa Moschatellina*!

Only the aecidial stage has been found in Scotland.

59. * Puccinia Asperulae-odoratae Wurth.

Trail, No. 19 (*Puccinia Galii* Pers. p.p.); Grove, p. 163.

Dee (Aberdeen), *Moray* (Dunphail, Blair Chapel and Forres).

I, II, III on *Asperula odorata*.

This species was collected by Trail near Aberdeen and by Keith near Forres; both the specimens are in the Herb. Trail.

60. * Puccinia punctata Link.

Trail, No. 19 (*Puccinia Galii* Pers. p.p.); Grove, p. 164.

Tweed (Berwick), *Forth*! (Pathhead and Aberlady), *Tay* (Pitlochry), *Dee* (Aberdeen), *Moray*! (Aviemore and Beauly).

Solway! (Thornhill and Stranraer), *Clyde* (West Kilbride), *Ross*! (Kintail).

0, I, II, III on *Galium verum*! *G. saxatile*! *G. palustre*! *G. uliginosum* and **G. Cruciata*!

The aecidial stage appears to be rare, but has been recorded from "Tay" on *G. verum* and also on *G. Cruciata* from Aberlady and Pathhead; this appears to be the first record of the aecidial stage on the host.

61. * Puccinia Celakovskyana Bubák.

Grove, p. 166.

Forth (Edinburgh and Culross).

0, II, III on **Galium Cruciata*.

A specimen in the Herb. Edin. collected by Greville and labelled *P. Valantiae* belongs to this species (see Hooker, Flora-Scottica, ii, p. 17). There is also a specimen in the Herb. Trail. with uredospores only, collected at Culross in 1889.

62. Puccinia Valantiae Pers.

Trail, No. 88; Grove, p. 167.

Tweed, Forth! Tay, Dee, Moray, Orkney.

Solway (Girvan and Moffat), Clyde, *Argyle* (Inveraray).

III on *Galium Cruciata*! and *G. saxatile*!

63. * Puccinia difformis K. et S.

Trail, No. 19 (*Puccinia Galii* Pers. p.p.); Grove, p. 168.

Moray! (Beauly), *Sutherland*! (Thurso).

I, III on *Galium Aparine*!

This species was recorded by Keith from several localities in "Moray" (Scot. Nat., n.s., i, 1883–4, p. 270). It was collected in 1925 at Beauly and in 1932 by J. R. Russell at Thurso. The only other British records appear to be from the south of England.

64. Puccinia Veronicae Schröt.

Trail, No. 91 (*P. Veronicae* Schum. p.p.); Grove, p. 169.

Tweed (Berwick), *Forth* (Edinburgh), *Moray*! (Beauly and Forres).

Solway (Girvan), *Clyde*! (Dunoon).

III on *Veronica montana*.

This species has been confused with *P. Veronicarum* DC. (*q.v.*, No. 65). The record for "Tweed" depends on that in Johnston's Flora of Berwick (ii, p. 194) where *P. Veronicarum* is given on the germander speedwell. This specimen is in the Herb. Kew. and is actually *P. Veronicae* on *Veronica montana*. The record for "Forth" is based on a specimen in the Herb. Kew., collected by Cooke in Roslin Woods in August 1871. The record for "Clyde" (Brit. Assoc. Flora and Fauna of Clyde Area) under *P. Veronicarum* probably refers to *P. Veronicae*, as *Veronica alpina*, the only known Scottish host of the former, does not occur in this area.

65. Puccinia Veronicarum DC.

Trail, No. 91, p.p.; Grove, p. 169.

Tay (Ben Alder and Perthshire).

III on *Veronica alpina*.

There are two specimens of the rust on *V. alpina* in the Herb. Kew. and these, as pointed out by Grove (p. 169), belong to *P. Veronicarum*. One in the Herb. Berkeley. is from Ben Alder, Inverness-shire (and also from Perthshire),

the other was collected by Rev. J. Fergusson and no locality is given. In both specimens the two forms of spores are present; one *fragilipes*, with deciduous pedicels, and the other *persistens*, with persistent pedicels. The sori are almost entirely on the leaves, generally on the upper surface; only few occur on the stems.

The teleutospore wall is thickened up to 10 μ at the apex.

The records given by Stevenson under *P. Veronicarum* DC. (No. 1225) in the Mycologia Scotica and by Trail (No. 91) under *P. Veronicae* Schum. are not included as these refer both to *P. Veronicae* and *P. Veronicarum*.

66. * Puccinia Porteri Peck.

Sydow, Monograph, i, p. 258.

Dee (Braemar).

Teleutospore sori hypophyllous or on the stems, sometimes epiphyllous, generally densely gregarious and often covering the whole surface of the leaf, rarely solitary, minute or medium sized, confluent, rounded or oblong or irregular, pulvinate, brown; teleutospores ellipsoidal or oblong, apex rounded or slightly attenuate, thickened up to 4–5 μ, slightly constricted, base generally rounded, smooth, pale brown, 24–38 × 14–22 μ; pedicel hyaline up to 40 μ long, easily deciduous.

III on * *Veronica alpina*.

This species has not been previously described as British and the only specimens found are those preserved in the Herb. Trail. These were collected by Buchanan White at the Corrie of Loch Kander, Braemar, in August 1886, and are probably those referred to in Scot. Nat., n.s., iii, 1887–8, p. 39. The sori of the rust are abundant on the lower internodes of the stems, spread up the petioles, and are occasionally found on the upper and lower leaf surfaces. The teleutospores are all of one kind and agree exactly with those of *P. albulensis* described by Magnus (Ber. deutsch. bot. Gesell., viii, 1890, p. 167). They differ from those of *P. Veronicarum* DC. in being rather shorter and wider, the thickening at the apex being less pronounced and forming an almost colourless papilla; the spore wall of the lower cell frequently shows a thickening in the vicinity of the germ-pore similar to that shown by Magnus in his drawings of the spores. As pointed out by Magnus, there is an abundant mycelium in the stem tissues in the vicinity

of the sorus, and the latter in its young condition is covered by at least two layers of cells of the host. On this account it is suggested that the rust exists as a perennial mycelium in the stem.

Sydow regards *P. albulensis* Magnus as identical with the North American species *P. Porteri* Peck, and accordingly this later name is adopted in his monograph.

67. Puccinia Menthae Pers.

Trail, No. 31; Grove, p. 170.

Tweed, Forth! Tay, Dee! Moray! *Orkney.*

Solway (Girvan and New Galloway), Clyde! *Argyle* (Inveraray), *Ross*! (Mallaig).

0, I, II, III on *Mentha aquatica*! *M. arvensis*! *M. rotundifolia*, *M. viridis*! *Origanum vulgare*! *Calamintha Clinopodium.*

This has been recorded on *Ajuga reptans* by Johnston in the Flora of Berwick and by Trail on *Thymus Serpyllum* from the Clyde area (Scot. Nat., iv, 1889–90, p. 59), but nothing further appears to be known of the forms on these hosts.

68. Puccinia caulincola Schneid.

Trail, No. 71 (*P. Schneideri* Schröt.); Grove, p. 172.

Tay, Dee.

Clyde (Largs).

III on *Thymus Serpyllum.*

This species has not been recorded from England. The record from Largs was made by Boyd (Glasgow Nat., i, 1909, p. 111). It was also collected at Loch Callater by L. Ogilvie in 1921, and plants were infected at Cambridge in 1922.

69. Puccinia Glechomatis DC.

Trail, No. 92; Grove, p. 173.

Forth! (Roslin), Tay.

Solway! (Creetown), *Clyde* (Ayr).

III on *Nepeta Glechoma*! and *Prunella vulgaris.*

It is doubtful whether the form on *Prunella vulgaris* recorded by Keith and Trail from Ben Lawers (Scot. Nat., ii, 1885–6, p. 331) really belongs to this species.

70. * Puccinia Betonicae DC.

Grove, p. 174.

Forth (Edinburgh).

III on **Stachys Betonica.*

This species was omitted by Trail from his list. The only record for Scotland is that by Greville in the Flora of Edinburgh.

71. Puccinia annularis Schlecht.

Trail, No. 97; Grove, p. 175.

Tweed! Forth, Tay! Dee, Moray!

Solway! (Girvan and Stranraer), Clyde, Argyle, Ross!

III on *Teucrium Scorodonia*!

72. Puccinia Vincae DC.

Trail, No. 36; Grove, p. 176.

Tay.

0, II, III on *Vinca* sp.

The only record for Scotland is by Fergusson from Maulesden and the host species is not stated.

73. Puccinia Primulae Duby.

Trail, No. 33; Grove, p. 179.

Tweed! (Cockburnspath), Forth, Tay, *Moray* (Drumnadrochit).

Solway! (Newton Stewart), Clyde, Argyle! *Ross*! (Mallaig).

I, II, III on *Primula vulgaris*!

74. Puccinia Soldanellae Fckl.

Trail, No. 34; Grove, p. 180.

Clyde.

0, I, II, III on *Soldanella alpina*.

This species has been found only in the Glasgow Botanic Gardens; only the aecidial stage was observed.

75. * Puccinia Hydrocotyles Cooke.

Grove, p. 181.

Clyde (Kilwinning).

I, II, III on **Hydrocotyle vulgaris*.

The rust was collected by Boyd at Kilwinning, Ayrshire, and this appears to be the only Scottish record.

The aecidial stage is not known from Britain.

76. Puccinia Saniculae Grev.

Trail, No. 35; Grove, p. 182.

Tweed, Forth! Tay, Dee, Moray.

Clyde! Argyle.

0, I, II, III on *Sanicula europaea*!

77. Puccinia Apii Desm.

Trail, No. 30; Grove, p. 184.

Tay.

0, I, II, III on *Apium graveolens*.

Only recorded once from Scotland, from Balnamoon, by Anderson.

78. Puccinia Aegopodii Mart.

Trail, No. 72; Grove, p. 185.

Tweed! Forth! Tay! Dee, Moray!

Clyde.

III on *Aegopodium Podagraria*!

79. Puccinia tumida Grev.

Trail, No. 78 (*P. Bunii* Wint.); Grove, p. 187.

Tweed! (Stobo), Forth, *Tay*! (Ballinluig), Dee, *Moray* (Forres).

Solway! (New Galloway), Clyde.

III on *Conopodium denudatum*!

80. Puccinia Pimpinellae Mart.

Trail, No. 29 (*P. Pimpinellae* Strauss, p.p.); Grove, p. 188.

Tweed! (Eyemouth), *Forth* (Balmuto), *Tay* (Kinloch Rannoch), *Dee* (Ellon), *Moray* (Aviemore).

Clyde (Glasgow).

0, I, II, III on *Pimpinella Saxifraga*!

81. * Puccinia Aethusae Mart.

0, I, II on *Petroselinum sativum*.

This is included on account of the statement made by Stevenson (M.S., No. 1316) that *Trichobasis petroselini* Berk. occurs "on Parsley." Trail includes it under *P. bullata* Pers., which he states is found on *Petroselinum sativum*. There is no mention of a rust on *P. sativum* in Greville's Flora Edin. or in Johnston's Flora of Berwick. No Scottish specimens have been seen.

82. * Puccinia Angelicae Fckl.

Grove, p. 192.

Forth (Aberfoyle), *Tay*! (Ballinluig).

0, II, III on * *Angelica sylvestris*!

83. * Puccinia Heraclei Grev.

Trail, No. 29 (*P. Pimpinellae* Strauss, p.p.); Grove, p. 194.
Forth! Tay! Dee, Moray, *Sutherland*! (Durness).
Clyde (Campsie), Argyle.
0, I, II, III on *Heracleum Sphondylium*!
This species was included in *P. Pimpinellae* by Trail.

84. * Puccinia Chaerophylli Purt.

Trail, No. 29 (*P. Pimpinellae* Strauss, p.p.); Grove, p. 195.
Tweed! (Stow), *Forth*! (Kinghorn and Pathhead), *Tay*! (Stanley), *Dee*! (Ballater), *Moray*! (Beauly), *Orkney*.
Argyle (Ardkinglas).
0, I, II, III on *Anthriscus sylvestris*! and *Myrrhis odorata*!
Included by Trail in *P. Pimpinellae*.

85. Puccinia Conii Fkcl.

Trail, No. 55 (*P. bullata* Pers. p.p.); Grove, p. 196.
Tweed! (Cockburnspath), *Forth*! (Pittenweem), *Dee* (Aberdeen).
II, III on *Conium maculatum*!

86. Puccinia Circaeae Pers.

Trail, No. 90; Grove, p. 198.
Tweed, Forth, Tay, Moray!
Solway (Thornhill), Clyde, Argyle.
III on *Circaea lutetiana*! and *C. alpina*.
This was recorded on *Circaea alpina* in Mull by Buchanan White in 1881 (Scot. Nat., vi, p. 162).

87. Puccinia pulverulenta Grev.

Trail, No. 26; Grove, p. 198.
Tweed! Forth! Tay! Dee! Moray, Orkney.
Solway (Lockerbie and Thornhill), Clyde!
0, I, II, III on *Epilobium montanum*, *E. hirsutum*! and * *E. parviflorum*!

88. Puccinia Epilobii DC.

Trail, No. 73; Grove, p. 200.
Tweed, Forth! Tay! Dee, *Moray*! (Kingussie).
Solway (New Galloway), Clyde! Argyle! *Ross*! (Mallaig).
III on *Epilobium palustre*! * *E. obscurum*! and * *E. alpinum*.

This rust was described on *E. obscurum* in 1924 (Trans. Brit. Mycol. Soc., ix, 1924, p. 137).

The record on *E. alpinum* was made by Gardiner in the Flora of Forfarshire (1848, p. 296) and has been overlooked in later lists; the specimens were collected at Loch Brandy, Glen Clova.

89. Puccinia Violae DC.

Trail, No. 27 and p. 367; Grove, p. 200.

Tweed! Forth! Tay! Dee! Moray! *Sutherland*! (Durness and Tongue), Orkney.

Solway! Clyde! Argyle! Ross!

0, I, II, III on *Viola canina*! *V. hirta*! * *V. odorata*! *V. Riviniana*! and *V. tricolor*.

90. Puccinia depauperans Sydow.

Trail, No. 27 (*P. Violae* Schum. p.p.) and No. 32 (*P. aegra* Grove); Grove, p. 202 (*P. aegra* Grove).

Forth! (Edinburgh and Markinch), Tay.

Solway! (Sandhead), *Clyde* (Glasgow and Troon).

0, I, II, III on *Viola tricolor*! *V. lutea* var. *amoena* and * *V. Curtisii* var. *Fosteri*!

The rusts on the *tricolor* group of Viola are here considered to belong to *P. depauperans*, although there appears to be no morphological difference between the spores of the latter and those of *P. Violae*.

Trail considered that *P. Violae* occurs on *V. tricolor* (see No. 89).

91. Puccinia Fergussoni B. et Br.

Trail, No. 80; Grove, p. 203.

Forth! (Dunblane), Tay, Dee! Moray!

Solway! (Sandhead), Clyde! *Argyle*! (Ben Cruachan), *Ross*! (Kintail and Skye).

III on *Viola palustris*!

92. Puccinia Buxi DC.

Trail, No. 96; Grove, p. 205.

Forth, Tay, Dee.

Solway! (Lockerbie and Girvan), *Argyle* (Inveraray).

III on *Buxus sempervirens*!

93. Puccinia Malvacearum Mont.

Trail, No. 89 and p. 367; Grove, p. 206.

Tweed! (Chirnside), *Forth*! (Edinburgh), Tay! Dee, *Moray* (Beauly, Aviemore, and Forres).

Clyde (Ayrshire), *Ross*! (Kintail).

III on *Malva sylvestris*! **M. moschata*! and **Althaea rosea*!

94. * Puccinia Pruni-spinosae Pers.

Grove, p. 207.

Forth! (Edinburgh), *Dee*! (Aberdeen).

Clyde (Seamill).

I on *Anemone coronaria*! *A. nemorosa*!

[II, III on *Prunus* sp.]

Only the aecidial stage of the rust appears to have been found in Scotland.

95. Puccinia Rhodiolae B. et Br.

Trail, No. 81; Grove, p. 210.

Tay, Dee, Moray.

III on *Sedum Rhodiola*.

96. * Puccinia Umbilici Guep.

Grove, p. 211.

Clyde! (Arran).

III on * *Cotyledon Umbilicus*!

97. * Puccinia Ribis DC.

Grove, p. 212.

Moray.

III on * *Ribes rubrum*.

The only record of this species is by Keith in Elginshire in 1894.

98. Puccinia Saxifragae Schlecht.

Trail, No. 83; Grove, p. 212.

Tay! (Ben Lui), Dee, *Sutherland*! (Ben Loyal).

Clyde! (Ben Bheula, Strachur), *Ross*! (Ben Attow).

III on *Saxifraga stellaris*!

99. * Puccinia Pazschkei Dietel.

Grove, p. 213.

Forth! (Edinburgh).

Clyde (Glasgow).

III on * *Saxifraga longifolia*! * *S. Hostii*! and its var. * *rhaetica*! * *S. aizoon* var. *cultrata*!

This is an introduced species recorded only on cultivated saxifrages (Trans. Brit. Mycol. Soc., vii, 1921, p. 81).

100. Puccinia Chrysosplenii Grev.

Trail, No. 87; Grove, p. 214.

Forth, Tay! Dee, Moray.

Solway! (Thornhill and Stranraer), Clyde, *Argyle* (Inveraray).

III on *Chrysosplenium oppositifolium*!

101. Puccinia Thalictri Chev.

Trail, No. 79; Grove, p. 214.

Tay, *Sutherland*! (Cape Wrath).

III on *Thalictrum minus* vars. *montanum* and * *dunense*!

This species was only once previously recorded from Scotland, by Trail from Kinloch Rannoch on *T. minus* var. *montanum*. The specimens from Cape Wrath were on var. *dunense*.

102. Puccinia fusca Wint.

Trail, No. 77; Grove, p. 215.

Forth! (Temple), Tay, Dee, Moray.

Solway, Clyde.

III on *Anemone nemorosa*!

103. Puccinia Calthae Link.

Trail, No. 21; Grove, p. 216.

Tweed, Forth, Tay! Dee, *Moray* (Aviemore), Orkney.

Clyde! (Brodick), *Ross*! (Mallaig).

0, I, II, III on *Caltha palustris*!

The records for Tweed, Forth, Dee, and Orkney are those given by Trail and may refer to *Puccinia Zopfii* (*q.v.*, No. 104); the aecidium collected at Brodick, which forms the record for Clyde, may also belong to *P. Zopfii*. Those for Tay, Moray, and Ross certainly refer to *P. Calthae*.

104. * Puccinia Zopfii Wint.

Grove, p. 217.

Tweed (Berwick and Westruther), *Tay*! (Tentsmoor), *Dee*! (Aberdeen and Lumphanan), *Sutherland*! (Tongue).

Solway! (New Galloway), *Clyde*! (Brodick), *Argyle*! (Taynuilt), *Ross*! (Skye).

0, I, II, III on * *Caltha palustris*!

This species is distinguished from *P. Calthae* by its broader, darker teleutospores which possess a few rather distant, minute warts towards the upper end and have short pedicels; the aecidial stages of the two species are indistinguishable, and in consequence the records for Tay and Clyde, where only aecidia were collected, may refer to *P. Calthae*.

105. Puccinia Lychnidearum Link.

Trail, No. 86 (*P. Arenariae* Schum.); Grove, p. 218.

Tweed! *Forth*! (Kirkcaldy), Tay! Dee, Moray, Orkney.

Solway! (Thornhill), *Clyde* (West Kilbride), *Ross*! (Arisaig).

III on *Stellaria media*! *S. Holostea*, * *S. graminea*! *S. uliginosa*, *Spergula arvensis*, *Lychnis diurna*! * *Arenaria trinervia*!

This species has not been previously recorded on *Stellaria graminea* in Britain. The specimen on this host was found in the Herb. Trail. and was collected at Forres on 16th October 1880; the pulvinate sori are found on the stems, leaves, and sepals and the teleutospores are almost unthickened at the apex. The rust was found on *Arenaria trinervia* by Trail at Crieff in 1889 and at the Scottish Cryptogamic Society's excursion at Blair-Atholl in 1906.

106. Puccinia Saginae K. et S.

Trail, No. 86 (*P. Arenariae* Schum.); Grove, p. 221.

Dee.

Clyde (West Kilbride).

III on *Sagina procumbens*, *S. nodosa*.

This species is frequently included in *P. Lychnidearum* (*q.v.*, No. 105). The specimens recorded from West Kilbride were found on the Scottish Cryptogamic Society's excursion in 1921.

107. Puccinia Silenes Schröt.

Trail, No. 22; Grove, p. 222 (*P. Behenis* Otth.).

Tweed (Berwick), Moray.

0, I, II, III on *Silene inflata* and *Lychnis diurna*.

The specimen from Berwick is in the Herb. Johnston. and

only bears uredospores. Specimens collected by Keith at Forres on *Lychnis diurna* in 1876 and on *Silene inflata* in 1881 are in the Herb. Trail.; these also bear only uredospores. Teleutospores have, however, been recorded by Trail.

108. * Puccinia Acetosae Körn.

Grove, p. 223.

Tweed! (Cove), *Forth* (Roslin), *Tay*! (Ballinluig), *Moray*! (Beauly).

Solway! (Drumlanrig and New Galloway), *Clyde*! (Kintyre), *Argyle*! (Oban).

II, III on **Rumex Acetosa*! and **R. Acetosella*.

This species was not recorded by Trail, probably on account of the fact that teleutospores have not been found in Scotland and in its uredospore condition it is easily confused with *Uromyces Acetosae*. The uredospores usually possess two germ-pores and have few and distant spines, while those of *U. Acetosae* are finely and densely verrucose with three germpores. *Rumex Acetosella* is a new British host for this species. A specimen on this host collected in Roslin Woods, near Edinburgh, in 1821 is preserved in the Herb. Edin.; another was recently collected at Taynuilt.

109. Puccinia Oxyriae Fckl.

Trail, No. 65; Grove, p. 224.

Tay! (Ben Lui), Dee!

Ross.

II, III on *Oxyria digyna*!

110. * Puccinia Conopodii-Bistortae Kleb.

Trail, No. 147 (*Aecidium Bunii* DC.); Grove, p. 225.

Forth, Tay.

I on **Conopodium denudatum*.

[II, III on *Polygonum Bistorta*.]

The evidence for the inclusion of this as a Scottish species rests on the statements made by Greville (Flor. Edin., p. 445) and Stevenson (M.S., No. 1360) that *Aecidium Bunii* DC. has occurred in Scotland on "*Bunium Bulbocastanum*" which was at one time commonly used as a synonym for *Conopodium denudatum*. The *Aecidium Bunii* recorded by Greville and Stevenson cannot be the aecidial stage of *P. Bulbocastani* Fckl., since the host of the latter (*Carum Bulbocastanum*) is

not known in Scotland. It is possible that the teleutospore stage of *Puccinia tumida* was referred to in error as *Aecidium Bunii*, but, as pointed out by Trail, Plowright was of opinion that the aecidium on *Conopodium denudatum* was distinct from the *Puccinia* on this host (Brit. Ured. and Ustilag., p. 270). No specimens of the aecidium on *C. denudatum* have been seen.

111. * Puccinia septentrionalis Juel.

Sydow, Monograph, i, p. 575.

Forth! (Ben Ledi), *Tay*! (Ben Lui), *Dee* (Glen Callater).

Clyde! (Ben Voirlich), *Argyle* (Laggan).

Spermogonia absent.

Aecidiospores.—Aecidia amphigenous, on swollen rather extensive dark-violet spots, numerous; pseudoperidia widely expanded, revolute.

Uredospores.—Sori hypophyllous, producing pale spots on the upper surface of the leaf, naked, soon becoming pulverulent; spores with echinulate brown wall, contents bright orange, about 20 μ in diameter, germ-pores 3–4.

Teleutospores.—Sori at first developed amongst the uredospores, but later in special dark brown sori, usually hypophyllous, occasionally epiphyllous; spores rather variable, elliptic ovate or pear-shaped, 28–48 μ × 13–23 μ; upper cell thickened at apex with a hyaline papilla of variable size, lower cell with a lateral germ-pore; wall smooth, chestnut-brown; contents colourless; pedicels deciduous.

I on leaves and all green parts of * *Thalictrum alpinum*! II, III on * *Polygonum viviparum* and by artificial infection on *P. Bistorta*!

The aecidial stage was first found on Ben Lui in June 1913 and the teleutospores in the same locality in October 1914. An unnamed specimen of the aecidial condition collected in 1845 by Greville in Glen Callater, Aberdeenshire, is preserved in the Herb. Edin., and one collected by Buchanan White in 1886 in the Corrie of Loch Kander, Braemar, in Herb. Trail. The rust has now been recorded from a number of the higher mountains in Scotland, at altitudes from 2000–3500 feet, where the two hosts are found in proximity (J. Bot., liii, 1915, p. 43; Trans. Brit. Mycol. Soc., vii, 1921, p. 79, and ix, 1924, p. 135). On the Continent the uredospore and teleutospore

stages have been recorded on *Polygonum Bistorta*. The latter is a typical lowland plant, the greatest altitude at which it has been recorded in Scotland being 600 feet, while its northern limit is given as Aberdeen–Isle of Skye (Watson, Cybele Britannica, ii, p. 332). *Thalictrum alpinum* rarely or never descends below 1500 feet in central Scotland, although it has been found at sea-level in the extreme north. It is in consequence highly improbable that *P. septentrionalis* should naturally occur on *P. Bistorta* in this country.

In order to determine the susceptibility of the later species aecidiospores from *Thalictrum alpinum* were placed on the leaves of *P. Bistorta* growing in the Royal Botanic Garden, Edinburgh, in 1923. In about three weeks typical uredospore sori of *P. septentrionalis* were produced on the under surface of the leaves.

It must be concluded, therefore, that the non-occurrence of *Puccinia septentrionalis* on *Polygonum Bistorta* in this country is not determined by the immunity of the latter species but by the distribution of the alternative host, *Thalictrum alpinum*.

112. Puccinia Polygoni-vivipari Karst.

Trail, No. 64 (*P. Bistortae* DC. p.p.); Grove, p. 226.

Tay! Dee, Moray.

II, III on *Polygonum viviparum*!

There are two species of *Puccinia* on *Polygonum viviparum*, *P. Polygoni-vivipari* Karst., and *P. septentrionalis* Juel, and it appears that there has been some confusion between the two.

Stevenson (M.S., No. 1223 as *P. Bistortae* DC., which is recognised as a synonym for *P. Polygoni-vivipari* Karst.) gives in his description of the fungus "Spots none"; there are, however, obvious yellow spots on the leaves attacked by *P. Polygoni-vivipari*, while in the case of *P. septentrionalis* the spots are inconspicuous or absent. In *P. Polygoni-vivipari* the teleutospores measure 20–30 × 15–20 μ and are obovate-oblong, rounded and not thickened above. In *P. septentrionalis* the teleutospores are 28–48 × 13–23 μ, and are elliptic ovate or pear-shaped, the upper cell being thickened at the apex with a hyaline papilla; the two species are therefore easily distinguished.

Probably the earliest known specimen of *P. Polygoni-vivipari* is that collected by Greville in 1822 at Mar Lodge (now

in Herb. Edin.) and labelled *Puccinia vivipari* in his handwriting; this name is much earlier than *P. Polygoni-vivipari* of Karsten, but is evidently a *nomen nudum*.

Stevenson (M.S., No. 1223) refers to specimens collected by Keith in Morayshire and Buchanan White in Glenshee.

There are three specimens in Herb. Trail. labelled *P. Bistortae* DC., all collected by Trail; one found at Braemar 28 8 79 is *P. Polygoni-vivipari*, the second found at Braemar 10–12 8 82, and the third found at Glen Callater, Braemar, 10 8 82 are both *P. septentrionalis*. Grove (British Rust Fungi, p. 226) refers to specimens collected by Trail at Braemar in August 1882, and states that the spores of these agree with those on a specimen of *P. viviparum* issued by Fuckel. Trail in 1915, in a letter to the author, stated that his specimens of *Puccinia Polygoni-vivipari* evidently differed from those of *P. septentrionalis* collected in Scotland. It appears, then, that while Trail undoubtedly collected both species he only carefully examined the specimens of *P. Polygoni-vivipari*.

Stevenson in giving the distribution of *P. Polygoni-vivipari* (*P. Bistortae* DC.) up to 1800 feet is probably correct. The specimens collected in the Tay Valley (J. Bot., lvii, 1919, p. 162) were at an altitude of about 400 feet. Grove refers to this as a purely alpine species, but this description is better suited to *P. septentrionalis* which is probably never found below 1800 feet.

It is possible that *P. Polygoni-vivipari* is a heteroecious species, for on the Continent Klebahn has described *P. Angelicae-Bistortae* with uredospores and teleutospores on *Polygonum Bistorta* and aecidia on *Angelica sylvestris*, and Semadini has infected *P. viviparum* with uredospores from *P. Bistorta*.

In the Tay Valley *P. Polygoni-vivipari* occurs in the vicinity of *Angelica sylvestris*, but no aecidia have been found on the latter.

Vleugel (Svensk Bot. Tidssk., v, 1911, p. 341) has described the occurrence of uredospore and teleutospore sori on the bulbils and suggests that the rust hibernates by this method.

113. Puccinia Polygoni-amphibii Pers.

Trail, No. 60 (*P. Polygoni* Pers.); Grove, p. 227.

Tweed, Forth! Tay! Dee, Moray.

Solway! (Newton Stewart and Girvan), Clyde! *Argyle*, (Inveraray).

[I on *Geranium pratense* and *G. sylvaticum*.]

II, III on *Polygonum amphibium* var. *terrestre*.

The aecidial stage has not been found in Britain.

114. * Puccinia Iridis Wallr.

Grove, p. 230.

Forth! (Edinburgh).

Clyde (Troon).

II, III on * *Iris Pseudacorus* and * cultivated species!

Recorded from the Edinburgh Botanic Garden and by the Scottish Cryptogamic Society from Troon in 1928.

115. Puccinia Asparagi DC.

Trail, No. 20; Grove, p. 233.

Forth.

0, I, II, III on *Asparagus officinalis*.

The only Scottish record is by Greville in the Flora Edin. (p. 429).

116. * Puccinia Prostii Moug.

Sydow, Monograph, i, p. 638.

Forth! (Edinburgh).

Spermogones.—Amphigenous, numerous, amongst the teleutospore sori, yellowish brown.

Teleutospores.—Sori amphigenous, at first forming large yellow, oval spots, which later become grey and finally open by a longitudinal split, surrounded by grey ruptured epidermis, dark brown or black; spores brown, scarcely constricted, covered with long hyaline spines 56–62 × 17–19 μ, epispore 2–3 μ thick; pedicels variable, shorter or longer than the spore, up to 80 μ in length, hyaline, deciduous.

0, III on * *Tulipa sylvestris*!

This is a South European species, probably introduced into Britain on the host plant. It was first recorded in England by Massee on cultivated tulips (Mildews, Rusts, and Smuts, 1913, p. 139) and was recorded at the Royal Botanic Garden, Edinburgh, in 1914 (Notes from Roy. Bot. Gar. Edin., vii, 1913–15, p. 219), where it had been probably introduced on bulbs of *T. sylvestris* from Italy. Although it has been present in the Botanic Garden since 1914, it has not spread

to cultivated tulips in its vicinity; there is probably a systemic mycelium, and as all attempts to germinate the teleutospores have failed it appears that the spread of the fungus has taken place only by the vegetative propagation of the host plant. The species is striking on account of its very large, spiny teleutospores.

117. Puccinia Porri Wint.

Trail, No. 23 and p. 367; Grove, p. 235.

Forth! (Edinburgh), Tay, Dee, *Orkney*.

Clyde! (Arran).

II, III on *Allium Schoenoprasum*! **A. porrum*! and *A. vineale*!

There is a specimen of this rust named by Greville *Uredo Porri* (*Uredo Alliorum*) collected by Capt. Wauch in 1822; it appears to be on cultivated leek. Only uredospores have been found on the leek, but teleutospores occur on the other host species. The records from Orkney are on *A. Schoenoprasum*.

118. Puccinia obscura Schröt.

Trail, No. 47; Grove, p. 236.

Tweed (Berwick), *Forth*! (North Berwick), Tay, Dee, *Moray*! (Aviemore), *Sutherland*! (Durness).

Solway! (Ballantrae), *Clyde* (Seamill), *Ross*! (Skye).

0, I on *Bellis perennis*!

II, III on *Luzula campestris*! and *L. sylvatica*!

119. Puccinia oblongata Wint.

Trail, No. 62; Grove, p. 238.

Tweed! Forth! Tay! Dee! Moray, Orkney.

Solway (Stranraer), Clyde, Argyle, Ross.

II, III on *Luzula campestris*! *L. pilosa*! and *L. sylvatica*!

The form on *L. sylvatica* has recently been distinguished as a separate species, *P. Luzulae-maximae* Diet. (see Grove and Chesters, Trans. Brit. Mycol. Soc., xviii, 1934, p. 270).

120. Puccinia Caricis Reb.

Trail, No. 42; Grove, p. 241.

Tweed! Forth! Tay! Dee, Moray.

Clyde, *Argyle*! (Taynuilt), *Ross*! (Mallaig).

0, I on *Urtica dioica*!

II, III on * *Carex hirta*! *C. paludosa*! * *C. pendula*! * *C. ampullacea*! * *C. glauca*! * *C. pallescens*!

C. glauca appears to be a new host for Britain.

The form on *Carex binervis* recorded by Plowright (Brit. Ured. Ustilag., p. 170) and Grove (p. 242) has not been experimentally shown to belong to *Aecidium Urticae*. It occurs frequently on moors far removed from any plants of *Urtica dioica*; teleutospores have not been found on this sedge, and the rust appears to winter by means of uredospores. Its distribution is given below:

Tweed! (Kelso), *Forth*! (Dunfermline), *Dee* (Aberdeen), *Clyde*! (Strachur), *Ross*! (Mallaig).

121. Puccinia dioicae Magn.

Trail, No. 45; Grove, p. 244.

Tay (Killin), Dee! Orkney.

0, I on *Cnicus palustris*!

[II, III on *Carex dioica*.]

Only the aecidial stage has been found in Britain.

122. Puccinia Pringsheimiana Kleb.

Trail, No. 140 (*Aecidium Grossulariae* Gmel.); Grove, p. 242.

Tweed, Forth! Tay! Dee, Moray.

Solway! (Annan), *Clyde*! (Jura), *Argyle*! (Mull), *Ross*! (Skye).

0, I on *Ribes Grossularia*! * *R. sanguineum*!

II, III on *Carex Goodenovii*! * *C. aquatilis*! (?).

This rust is widespread in Scotland and produces a rather serious disease of the gooseberry, the aecidia appearing on the leaves, petioles, and fruits. Teleutospores from *C. Goodenovii* placed on the gooseberry on 10th April 1931 produced aecidia on 23rd April. Aecidia were found on the leaves and fruits of *Ribes sanguineum*, a new British host for the species, in Skye in July 1932, but at this date all the spores had been shed; they have recently been found on the same host in Mull.

Plants of *C. aquatilis* bearing uredospores and teleutospores were found at Thornhill, near Stirling, close to heavily infected gooseberries, but no experimental infections have been carried out and it is not certain that this sedge is a host species.

Klebahn has also infected *R. rubrum*, *R. alpinum*, and *R. aureum*, but was unable at first to infect *R. nigrum* (Pringsh. Jahrb., xxxiv, 1899, p. 388); later, however, he was able to infect this last species (Zeitschr. Pflanzenkrankh., xli, 1931, p. 209), but he believed this to be an instance of incomplete adaption to an originally uncongenial host. He gives *Carex Goodenovii* Gay, *C. acuta* L., *C. stricta* Good., and *C. caespitosa* L. as teleutospore hosts (Pringsh. Jahrb., xxxv, 1900, p. 703); the last is not a British species.

Grove queries the occurrence of this rust on *R. nigrum*, but it has recently been described on this species in Norfolk by Dillon Weston (Min. of Agric. Monthly Rpt., Diseases, No. 6, 1932).

123. Puccinia silvatica Schröt.

Trail, No. 44; Grove, p. 245.

Tweed, Forth, Tay, Dee, Moray.

0, I on *Taraxacum officinale*, *T. palustre*.

[II, III on *Carex* sp.]

A specimen in the Herb. Trail. collected in Aberdeen in July 1879 and one in the Herb. Johnston. found at Berwick appear to belong to this species. G. K. Sutherland has recorded it on *T. palustre* at Aberdeen. The uredospore and teleutospore stages have not been found in Britain. The aecidia are in large round clusters in this species, while those of *P. variabilis* (No. 51) are in small clusters with single ones scattered between.

124. Puccinia Schoeleriana Plowr.

Trail, No. 43; Grove, p. 246.

Forth! Tay! Dee.

Solway! (Sandhead), Clyde.

0, I on *Senecio Jacobaea*!

II, III on *Carex arenaria*!

This was at one time supposed to be confined to the east coast of Britain, but has been found in abundance at Sandhead, Wigtownshire, and has been recorded for the Clyde area in the British Association list. Aecidia of this species and teleutospore sori of *P. glomerata* (No. 35) may be found on the same leaf of *Senecio Jacobaea*.

125. Puccinia paludosa Plowr.

Trail, No. 46; Grove, p. 248.

Tweed (Berwick), Tay, Dee, *Sutherland*! (Tongue), Orkney.

Clyde (Ardrossan), *Argyle*! (Taynuilt), *Ross*! (Kintail).

0, I on *Pedicularis palustris*!

II, III on *Carex Goodenovii*! and *C. fulva*.

Although this species is not included in Johnston's Flora of Berwick there is a specimen of the aecidial stage in his herbarium, but no locality is given and the specimen is not labelled in his handwriting. The aecidial stage was recorded from Taynuilt in 1924 (Trans. Brit. Mycol. Soc., ix, 1924, p. 136), and teleutospores were found on *C. Goodenovii* at Tongue in the vicinity of plants of *P. palustris* in 1931. The record from the Clyde area is from the British Association list.

126. Puccinia uliginosa Juel.

Trail, No. 9 (*Uromyces Parnassiae* DC.); Grove, p. 249.

Tweed (Lammermuir Hills), Forth, Tay, Dee, *Orkney*.

Clyde! Argyle! (Taynuilt).

I on *Parnassia palustris*!

[II, III on *Carex Goodenovii*.]

Only the aecidial stage has been found in Britain. There is a specimen in the Herb. Johnston. labelled " Lammermuirs, M. J. B "(erkeley). It is recorded from Orkney by Grove and by G. K. Sutherland.

127. Puccinia graminis Pers.

Trail, No. 37; Grove, p. 250.

Tweed! Forth! Tay, Dee, Moray! Orkney.

Solway! (Thornhill), Clyde, *Argyle*! (Tyndrum), Ross.

0, I on leaves and fruits of *Berberis vulgaris*! and *B. Aquifolium*.

II, III on *Avena sativa*! * *A. strigosa*, *Arrhenatherum elatius*, *Festuca pratensis*, *Triticum vulgare*! * *Hordeum vulgare*, *H. distichum*, * *Agropyrum repens*! * *Agrostis vulgaris*! * *A. alba*, * *Alopecurus pratensis*! * *Dactylis glomerata*! * *Aira caespitosa*, * *Secale cereale* and * *Bromus sterilis*.

The occurrence of the aecidia on *Mahonia aquifolia* was recorded by Berkeley and Broom (Notices Brit. Fungi, No. 1469) and by Stevenson at Glamis.

It was recorded on *Avena strigosa* and *Aira caespitosa* by Sutherland.

An account of the distribution of the rust in Scotland has been published by Maxwell and Wallace (Trans. Brit. Mycol. Soc., xi, 1926, p. 138). In this it is concluded that the following specialised forms of the rust are found in Scotland:—

Puccinia graminis Tritici on *Triticum sativum*.

Puccinia graminis Avenae on *Avena sativa*, *Secale cereale*, (*Alopecurus pratensis* and *Dactylis glomerata*).

Puccinia graminis Secalis on *Secale cereale*, *Hordeum vulgare* and *Agropyrum repens*.

Puccinia graminis Agrostidis on *Agrostis vulgaris* and *A. alba*.

There is no experimental proof that the forms on *Alopecurus pratensis* and *Dactylis glomerata* belong to *P. graminis Avenae*, but they have been found associated with this form.

To these must probably be added:

Puccinia graminis Airae on *Aira caespitosa*.

Puccinia graminis Arrhenatheri on *Arrhenatherum elatius*.

128. * Puccinia Phlei-pratensis Erikss. et Henn.

Grove, p. 283.

Clyde! (Ayr).

II, III on * *Phleum pratensis*! and * *Festuca elatior*.

This is separated from *P. graminis* on the ground that it will not infect *Berberis communis*.

Boyd (Rpt. Scot. Crypt. Soc., 1926) records its occurrence on *Avena sativa*, but it appears that the form on this host belongs to *Puccinia graminis*. This species is stated to occur on *Dactylis glomerata*, but the form found in Scotland on this host is probably *P. graminis* (see No. 127). The form on *Festuca pratensis* recorded by Trail under *P. graminis* should possibly be included here.

129. Puccinia coronata Corda.

Trail, No. 38 (*P. coronata* Corda, p.p.); Grove, p. 253.

Orkney.

Solway! (New Galloway), *Argyle*! (Taynuilt).

0, I on * *Rhamnus Frangula*!

II, III on *Agrostis stolonifera*! *A. vulgaris*!

The aecidial stage was recorded from Holland Isle, New

Galloway, by Scott Elliot in 1924 (Dumfriesshire and Galloway Nat. Hist. Soc. Trans., ser. 3, xi, 1925, p. 85) and has recently been found in the same locality.

130. * **Puccinia Lolii** Nielsen.

Trail, No. 38 (*P. coronata* Corda, p.p.); Grove, p. 255.

Tweed! (Peebles and Coldingham), *Forth*! (Edinburgh, Burntisland, and North Berwick), *Tay*! (Ballinluig and Brechin), *Dee* (Aberdeen), *Moray*! (Aviemore and Forres), *Orkney*.

Solway! (New Galloway and Gatehouse), *Clyde*! (Ayr and Arran), *Ross*! (Skye).

0, I on * *Rhamnus catharticus*.

II, III on * *Avena sativa*! * *A. strigosa*, * *Arrenatherum elatius*! * *Festuca elatior*! * *Dactylis glomerata*, * *Lolium perenne*! * *Aira caespitosa*!

The aecidial stage was found in the Botanic Garden, Aberdeen, in 1926.

The record on *Avena strigosa* is from Orkney.

The occurrence of this rust on *Aira caespitosa* has been recorded by Sydow (Monograph, i, 704); it has been known on this host for some time in Scotland in the uredospore condition, and teleutospores were found for the first time at Brechin in November 1933. When in the uredospore condition it may be distinguished from *Uredo Airae* on the same host (see No. 232) by its more abundant, bright yellow sori, which occur on both sides of the leaves and also on the stems and sheaths, and by the absence of the paraphyses.

131. Puccinia Festucae Plowr.

Trail, No. 141 (*Aecidium Periclymeni* Schum.); Grove, p. 257.

Tweed, Forth! Tay, Dee, Moray.

Clyde! Argyle!

0, I on *Lonicera Periclymenum*!

II, III on * *Festuca ovina*, * *F. rubra* var. *arenaria* Osb.

Only the aecidial stage was recorded by Trail. The specimen on *F. rubra* var. *arenaria* was collected at Oban.

132. * **Puccinia longissima** Schröt.

Trail, No. 74 and p. 367 (*P. paliformis* Fckl.); Grove, p. 286 (*P. paliformis* Fckl.).

Tay, Dee, *Moray* (Cullen).

[*Spermogonia*.—Scattered, rather large.

Aecidiospores.—Aecidia solitary over the whole leaf, deeply immersed, hemispherical, opening with a minute median pore, yellow; spores globose or ellipsoid, mostly angular, verruculose, orange, 22–32 × 18–30 μ.]

Uredospores.—Sori epiphyllous, arranged in rows or little groups between the nerves, marked on the lower surface by discoloured spots, oblong, about ·5 mm. in length, surrounded by the ruptured epidermis, deep orange-brown, at length pulverulent; spores ovoid or roundish, rather thin-walled but provided with several scattered thickened areas (pores), about 25–30 μ in diam., finely echinulate with orange contents and a yellowish or pale-brown coloured membrane.

Teleutospores.—Sori similar but narrower, often more lanceolate, surrounded and partly covered by the cleft epidermis, at length naked but not pulverulent, deep chestnut-brown; spores elongate, oblong or subclavate, yellowish-brown, 60–120 × 12–20 μ; upper cell ellipsoid or cylindrical, thickened above (up to 10 μ) where it is rounded or attenuated to a blunt (sometimes oblique) point, darker, *i.e.* chestnut-brown; the lower cell usually cylindrical, mostly longer than the upper one (by as much as one-third), paler and narrower, sometimes, especially when shorter, attenuated downwards and obovoid or pyriform, thin walled, a constriction at the darker septum or none, short, pale brown.

[I on *Sedum acre*.]

II, III on *Koeleria cristata*.

The rust on *Koeleria cristata* was for some time regarded by Trail and Grove as *P. paliformis*, but as the result of the discovery of fresh material by the former in 1916 near Aberdeen (Grove, J. Bot., lv, 1917, p. 134) it was found to be practically identical with *P. longissima*, as described by Bubák (Centralbl. Bact. Parasitenk., 2 Abt., ix, 1902, pp. 126 and 922). The aecidial stage has not been found in Britain, but on the Continent it has been described on *Sedum acre* and *S. boloniensis*; the former is a common British species, and further search may lead to the discovery of the fungus upon it.

133. * Puccinia glumarum Erikss. et Henn.

Trail, No. 40 (*P. rubigo-vera* DC. p.p.); Grove, p. 258.

Tweed! (Coldingham and Berwick), *Forth*! (Edinburgh,

Pathhead and North Berwick), *Tay*! (St. Andrews and Leuchars), *Dee* (St. Cyrus), *Orkney*.

II, III on *Triticum vulgare*! **Hordeum murinum*! **H. vulgare*! * *Agropyrum repens*! **Elymus arenarius*!

Hordeum murinum is a new British host for this rust (Trans. Brit. Mycol. Soc., ix, 1924, p. 137). It was recorded from Orkney by G. K. Sutherland.

134. * Puccinia secalina Grove.

Trail, No. 40 (*P. rubigo-vera* DC. p.p.); Grove, p. 261.

Tweed, *Forth*! (Pathhead), Tay.

0, I on *Anchusa arvensis*.

II, III on *Secale cereale*.

There is a specimen of the aecidial stage in the Herb. Johnston. Only the uredospores and teleutospores have been found at Pathhead.

135. * Puccinia bromina Erikss.

Trail, No. 40 (*P. rubigo-vera* DC. p.p.); Grove, p. 262.

Forth! (Pathhead), *Tay*, *Dee*.

Solway! (Newton Stewart), *Clyde* (Glasgow).

[0, I on *Symphytum officinale*.]

II, III on **Bromus sterilis*! * *B. giganteus*! **B. mollis*.

Only the uredospore and teleutospore stages have been found in Scotland.

136. * Puccinia triticina Erikss.

Trail, No. 40 (*P. rubigo-vera* DC. p.p.); Grove, p. 262.

Tweed! (Coldingham).

II, III on **Triticum vulgare*!

This appears to be the only record from Scotland, although the rust is common in England where it causes a serious disease of wheat.

No aecidial stage is known in Britain, but both on the Continent and in North America it has been shown that this species is heteroecious and forms its aecidium on *Thalictrum* sp.

137. * Puccinia holcina Erikss.

Trail, No. 40 (*P. rubigo-vera* DC. p.p.); Grove, p. 263.

Tweed! (Berwick and St. Mary's Loch), *Forth*! (Edinburgh and North Berwick), *Tay*! (Ballinluig), *Dee*! (Lum-

phanan), *Moray*! (Beauly and Aviemore), *Sutherland*! (Durness), *Orkney*.

Solway! (Thornhill), *Clyde*! (West Kilbride and Arran), *Ross*! (Mallaig).

II, III on *Holcus lanatus*! and *H. mollis*!

138. * Puccinia agropyrina Erikss.

Trail, No. 40 (*P. rubigo-vera* DC. p.p.); Grove, p. 263.

Tweed! (Cove), *Forth*! (Edinburgh and North Berwick), *Tay*! (Montrose), *Dee* (Aberdeen and Ballater).

Clyde (West Kilbride).

II, III on *Agropyrum repens*!

139. * Puccinia Triseti Erikss.

Grove, p. 264.

Tweed! (Coldingham) *Forth*! (Pathhead, Burntisland), *Tay*! (Ballinluig).

II, III on **Trisetum flavescens*!

140. * Puccinia simplex Erikss. et Henn.

Trail, No. 40 (*P. rubigo-vera* DC. p.p.); Grove, p. 264.

Tweed! (Coldingham), *Forth*! (Pathhead).

II, III on *Hordeum vulgare*!

141. * Puccinia Orchidearum-Phalaridis Kleb.

Trail, No. 51 (under *P. Moliniae* Tul.); Grove, p. 268.

Tay.

0, I on *Orchis latifolia*.

II, III on *Digraphis* (*Phalaris*) *arundinacea*.

The only definite record of this rust rests on the discovery of *Aecidium Orchidearum* by Fergusson at Monikie.

142. * Puccinia Winteriana Magn.

Trail, No. 39 (*P. sessilis* Schneider); Grove, p. 268.

Tweed! Forth, *Dee* (Aberdeen).

Solway! (Thornhill and Allanton), Clyde!

0, I on *Allium ursinum*.

II, III on *Digraphis* (*Phalaris*) *arundinacea*!

Trail's records refer only to the aecidial stage. There is a specimen of the latter in the Herb. Johnston. from Dulaw Dean, Berwickshire, and it was collected here in June 1933. Specimens of the uredospore and teleutospore stages are found in the Herb. Trail. from Aberdeen and have been collected at

Thornhill, Allanton, and in Arran; these may, however, belong to *P. Orchidearum-Phalaridis* (No. 141).

143. * Puccinia borealis Juel.

Trail, No. 146 (*Aecidium Thalictri* Grev.).

Forth, Tay! Dee, Moray.

Clyde (Ben Voirlich).

Aecidiospores.—Aecidia hypophyllous, in groups of 8–12, seated on unthickened spots which become pale or reddish on the upper surface, white or pale yellow, at first cylindrical, later with torn revolute margins; spores subglobose or angular, finely punctate, orange, 13–18 μ.

[*Uredospores.*—Sori mostly epiphyllous, oblong, seated on pale spots, soon naked, orange; spores globose or subglobose, delicately echinulate, yellow, 18–22 μ.

Teleutospores.—Sori hypophyllous, covered by the epidermis, small, linear often fused, black; spores clavate or subclavate, apex usually truncate, rarely slightly attenuate, wall uniformly thick (up to 5 μ), base attenuate smooth, brown, 35–45 × 13–20 μ; pedicels very short, hyaline.]

I on *Thalictrum alpinum*!

[II, III on *Anthoxanthum odoratum* ?.]

This rust, although described by Greville in his Scottish Cryptogamic Flora as *Aecidium Thalictri* and included by Stevenson and Trail, appears to have been omitted from later lists of British rust fungi.

Stevenson, in its distribution, gives the district "Forth," although it is omitted by Trail.

The type specimen of *Aecidium Thalictri*, collected on Ben Voirlich (Loch Lomond) in 1823 and named by Greville, is in the Herb. Edin. In 1914 a search for the rust on this mountain was unsuccessful, but the aecidial stage was found on Ben Lui in 1919 (J. Bot., liii, 1915, p. 44; and lvii, 1919, p. 162).

Uredospores and teleutospores have not been found in Great Britain, and the host of these spore stages is uncertain. The rust has been found on *Agrostis* sp., *Calamagrostis stricta*, *Hierochloe odorata*, *Anthoxanthum odoratum*, and *Deschampsia caespitosa* in Iceland by Rostrup (Bot. Tidsskrift, 1903, p. 290). In Norway it is recorded by Jorstad (Nyt Magazin for Naturvidenskaberne, lxx, p. 334) on *Agrostis*

borealis Hn., *A. capillaris* L. (*A. vulgaris* With.), *Anthoxanthum odoratum* L., *Hierochloe odorata* Wg., and *Calamagrostis neglecta* Ehrh.

The aecidial stage of *P. septentrionalis* which also occurs on *Thalictrum alpinum* is distinguished by the extensive swollen dark violet spots that it produces on the leaves, petioles, and sometimes on the stems. The two aecidial stages have been found closely associated on Ben Lui.

144. *Puccinia Anthoxanthi Fckl.

Grove, p. 269, p.p.

Dee! (Aberdeen).

Solway! (Gatehouse).

II, III on **Anthoxanthum odoratum*!

This species has been confused with *Uredo anthoxanthina* (see No. 230). It was suggested in 1915 (J. Bot., 1915, p. 47) that two distinct rusts existed in this country on *A. odoratum*, and in 1921 (J. Bot., 1921, p. 311) Grove recorded *P. Anthoxanthi* and *U. anthoxanthina* from England. The former was first found in Scotland in 1924 (Trans. Brit. Mycol. Soc., ix, 1924, p. 138). *P. Anthoxanthi* usually produces both uredospores and teleutospores, the former being without paraphyses, while in *U. anthoxanthina* only uredospores mixed with numerous capitate paraphyses are found.

145. * Puccinia Arrhenatheri Erikss.

Grove, p. 284.

Tweed! (Peebles), *Forth*! (Edinburgh), *Tay*! (Montrose and Tayport).

Moray! (Beauly), *Sutherland*! (Durness).

Solway! (Carronbridge), *Clyde* (West Kilbride).

[I on *Berberis vulgaris*.]

II, III on **Arrhenatherum elatius*!

As pointed out by Grove this rust appears to be identical in its uredospore and teleutospore stages with the continental specimens of *P. Arrhenatheri*, but the aecidial stage has not been found in this country and no infection experiments with British specimens appear to have been carried out. The rust has now been under observation for several years in Edinburgh, where it is growing in the vicinity of a barberry bush, but no infection of the latter has occurred. It is

possible that the rust has completely lost its aecidial stage in this country.

The parasite *Darluca Filum* is often found in the sori.

146. Puccinia perplexans.

Trail, No. 52; Grove, p. 270.

Dee.

I on *Ranunculus acris*.

II, III on *Alopecurus pratensis*.

The only record of this rust for Scotland appears to be that of Brebner who collected all the stages at Aboyne.

147. Puccinia Magnusiana Körn.

Trail, No. 50; Grove, p. 271.

Tweed, Forth, *Tay*! (Montrose).

Solway! (Gatehouse and New Galloway).

I on *Ranunculus repens*!

II, III on *Phragmites communis*!

Trail stated that he knew nothing of this as a Scotch fungus and only included it in his list on the authority of Plowright (Brit. Ured. and Ustilag., p. 177), who in turn quoted Greville (Flor. Edin., pp. 433 and 446) and Johnston (Flor. Berw., ii, pp. 195 and 206) as authorities for its inclusion. Greville gave *Aecidium Ranunculacearum* DC. from Duddingston Loch and Roslin Woods on *Ranunculus Lingua* and *R. acris*, but these probably did not belong to *P. Magnusiana* as Plowright and others have failed to infect these species in culture. Johnston gave *Aec. Ranunculacearum* on *R. acris* and *R. repens*, and that on the latter host may belong to this species. Although Trail (following Plowright) gave *R. bulbosus* as a host there appears to be no Scottish record on this species. Both Greville and Johnston record *P. graminis* var. *arundinis* (a synonym for *P. Magnusiana*) from Edinburgh and Berwick respectively.

Uromyces Poae and *U. Dactylidis* also form their aecidia on *Ranunculus repens* and *R. bulbosus* and are morphologically indistinguishable, but appear in March to May, those of *P. Magnusiana* developing in June or July.

There are two specimens of this species on *Phragmites communis* in the Herb. Edin., one collected by Greville in 1821, no locality being given, and the other by A. B. at Pitfour, near Perth, in 1845. There is also a specimen bearing

uredospores and teleutospores in the Herb. Trail., collected at Longforgan, Gowrie, in 1889.

Specimens of aecidia on *R. repens* were collected at Usan, near Montrose, in July 1930, and the aecidiospores placed on leaves of *Phragmites communis* produced uredospore sori in about twelve days and, later, teleutospores. Uredospores and teleutospores were collected in August from the same locality; they have also been found in the Solway area.

P. Magnusiana may be distinguished from *P. Phragmites* and from *P. Trailii* by its numerous small teleutospore sori and by the presence of numerous paraphyses among the uredospores.

148. Puccinia Phragmitis Körn.

Trail, No. 48; Grove, p. 273.

Tweed (Berwick), Forth, Tay, *Dee* (Aberdeen), *Moray*.

Solway! (Dumfries and Gatehouse).

0, I on *Rumex crispus*!

II, III on *Phragmites communis*!

149. Puccinia Trailii Plowr.

Trail, No. 49; Grove, p. 274.

Tweed! (Coldingham), Dee.

Solway! (Dumfries).

0, I on *Rumex Acetosa*!

II, III on *Phragmites communis*!

There is a specimen of the aecidial stage labelled by Greville "Scottish Highlands, Trevelyan" in the Herb. Edin.

150. * Puccinia Agrostidis Plowr.

Grove, p. 275.

Tay! (Dunkeld), *Dee* (Ballater), *Moray*! (Forres).

Solway! (Dalry).

0, I on * *Aquilegia vulgaris*.

II, III on * *Agrostis vulgaris*! *A. alba*! *A. stolonifera*!

There is a specimen of the aecidial stage in the Herb. Trail. collected at Ballater in 1891. The uredospore and teleutospore stages were found at Dunkeld and Dalry.

151. Puccinia Brunellarum-Moliniae Cruchet.

Trail, No. 51 (*P. Moliniae* Tul.); Grove, p. 277 (*P. Moliniae* Tul.).

Tay! Moray.

Clyde, Argyle! *Ross*! (Arisaig).

I on *Prunella vulgaris*.

II, III on *Molinia caerulea*!

There is some doubt as to the species of the *Puccinia* occurring on *Molinia caerulea* in Scotland, but it appears probable that it is *P. Brunellarum-Moliniae* as *Aecidium Prunellae* Wint. has been found twice in the country, the first time by Keith at Forres (Plowright, Brit. Ured., p. 264) and later by D. A. Boyd at Killin in 1891 (Glasgow Nat., iii, 1889–92, p. xxxii). Also it has been noticed that in at least two situations where the teleutospores were found *Prunella vulgaris* was common (Trans. Brit. Mycol. Soc., vii, 1920–1, p. 82). Trail, following Rostrup and Plowright, believed that the aecidial stage occurred on *Orchis*, but this appears to be a mistake. Juel and Liro have shown that an aecidium on *Melampyrum* is part of the life-cycle of a *Puccinia* on *Molinia*, but this aecidium has not been found in Britain.

152. Puccinia Poarum Niels.

Trail, No. 41; Grove, p. 278.

Tweed! Forth! Tay! Dee, Moray! Orkney.

Solway! (Creetown), Clyde! Argyle.

0, I on *Tussilago Farfara*!

II, III on *Poa pratensis*! *P. nemoralis*! *P. trivialis*!

This species was recorded by Keith (Scot. Nat., i, 1883–4, p. 270) on *Glyceria fluitans* at Grantown, but there appears to be no other record on this host.

153. Puccinia Baryi Wint.

Trail, No. 63; Grove, p. 280.

Tweed! (Cove), Forth! Tay! Dee.

Solway! (Newton Stewart), *Clyde*! (West Kilbride and Arran), *Argyle* (Inveraray).

II, III on *Brachypodium sylvaticum*!

154. Puccinia persistens Plowr.

Trail, No. 53; Grove, p. 282.

Dee.

0, I on *Thalictrum minus* var. *dunense*.

[II, III on *Agropyrum repens*.]

Trail found uredospores and teleutospores of what he

believed to be this species growing on *Festuca rubra* close to the aecidium, but there is no record of the fungus on this host. Apart from this there appears to be no record of the uredospore and teleutospore stages in Scotland.

155. Puccinia (Uropyxis) mirabilissima Peck.

Sydow, Monograph, i, p. 844.

Tweed! (Peebles and Berwick), *Forth*! (Edinburgh), *Tay*! (Murthly and Pitlochry).

Solway! (Moffat, Lockerbie, and Thornhill), *Clyde*! (Dunoon).

Spermogonia.—Generally epiphyllous, occasionally hypophyllous, on thickened spots, yellowish-brown.

Aecidiospores.—Aecidia generally hypophyllous, opposite the spermogonia, occasionally epiphyllous, on thickened greenish-black spots, from four to a large number in a group; pseudoperidia yellow, rather shortly and widely cylindrical (about 9 μ in diam.) with recurved, much cut margin, consisting of cells about 22·7 × 18·4 μ with strongly thickened, pitted outer walls; aecidiospores rather pale orange-yellow, angular-globose or ovate, very finely echinulate, 23·5–17·7 × 21·2–15·4 μ, mean 20·48 × 19·13 μ.

Uredospores.—Sori hypophyllous seated on small red or purple spots, scattered or in small groups, minute, compact, pale brown; spores subglobose, ovate or pyriform, minutely echinulate, pale brown, 22–38 × 16–24 μ, wall thick, with 2–6 germ-pores; pedicels long and colourless joined to the spore by a distinct articulation and persistent in the sorus after the spore has fallen.

Teleutospores.—Few, scattered amongst the uredospores and projecting beyond them, ellipsoid or oblong-ellipsoid, rounded at both ends, apex not thickened, constricted at the septum; the wall consists of four layers; (1) the innermost is thin and dark coloured, (2) a thick brown warted layer, (3) hyaline layer, (4) the outermost, a very fine cuticularised layer; germ pores two in each cell, about in the middle of the walls and all in the same plane; 30–36 × 20–25 μ; pedicels hyaline often obliquely inserted, up to 200 μ long, persistent, very thick walled and swollen at the base.

0, I, II, III on *Berberis Aquifolium*!

The aecidia (Ann. Mycolog., xxviii, 1930, p. 225) are found

on the young leaves which at that time do not bear the other spore stages. They are distinguished from those of *Puccinia graminis*, which may occur on the same host, by the distinctly yellow pseudoperidia. No infection experiments have been carried out, but the frequent association of these aecidia with the other spore stages makes it almost certain that they belong to *P. mirabilissima*.

This rust was discovered near Edinburgh in 1922 (Trans. Bot. Soc. Edin., xxviii, 1923, p. 164, and Trans. Brit. Mycol. Soc., ix, 1924, p. 135), this being the first European record. It is now widespread in southern Scotland, extending as far north as Pitlochry, and has been recorded from Northumberland, Wales, and recently from the south of England. It is a North American species, found in Utah, Colorado, and Montana on *Berberis repens* and other species. There is some evidence that it may have been introduced into the Tweed Valley from North America. Since 1922 it has been recorded from Holland, Denmark, Germany, Latvia, and France, and it appears to be spreading rapidly in Europe, especially in an eastward direction.

TRIPHRAGMIUM Link.

156. Triphragmium Ulmariae Wint.

Trail, No. 98; Grove, p. 287.

Tweed! Forth! Tay! Dee! Moray! *Sutherland*! (Tongue), Orkney.

Solway! (Thornhill), Clyde! *Argyle*! (Inverliever and Taynuilt), *Ross*! (Skye).

II, III on *Spiraea Ulmaria*!

PHRAGMIDIUM Link.

157. Phragmidium Fragariastri Schröt.

Trail, No. 99; Grove, p. 290.

Tweed! Forth! Tay! Dee, Moray!

Solway! (Lockerbie and Girvan), Clyde! Ross!

0, I, II, III on *Potentilla Fragariastrum*!

158. Phragmidium Potentillae Karst.

Trail, No. 100; Grove, p. 201.

Forth.

0, II, III on *Potentilla argentea*.

The only Scottish record appears to be that of Greville (Flor. Edin., p. 428, and Crypt. Flora, i, p. 57).

159. Phragmidium disciflorum James.

Trail, No. 104 (*P. subcorticatum* Schr.); Grove, p. 293.

Tweed! Forth! Tay! Dee, Moray! Orkney.

Solway! (Thornhill and Lockerbie), Clyde, Argyle, Ross!

0, I, II, III on *Rosa canina*! *R. mollis*, * *R. involuta*! * *R. spinosissima*! *R. tomentosa*, and cultivated roses.

160. Phragmidium fusiforme Schröt.

Trail, No. 105 (*P. Rosae-alpinae* DC.); Grove, p. 294.

I, II, III on *Rosa alpina*.

The inclusion of this species as a Scottish rust rests on the record given by Plowright (Brit. Ured. Ustilag., p. 226). No locality is given. No British specimens are known in herbaria.

161. Phragmidium violaceum Wint.

Trail, No. 102; Grove, p. 295.

Tweed, Forth, Tay! Dee! Moray!

Solway! Clyde! Argyle, Ross!

0, I, II, III on *Rubus fruticosus*! *R. corylifolius*.

162. Phragmidium Rubi Pers.

Trail, No. 103, p.p.; Grove, p. 297.

Tweed (Berwick), *Forth* (Edinburgh), Tay! Dee, *Moray*! (Beauly), Orkney.

Clyde! (Arran), *Argyle* (Mull), *Ross*! (Mallaig).

0, I, II, III on *R. fruticosus*! *R. corylifolius*.

This species is frequently found near the sea, while *P. violaceum* is generally distributed.

163. * Phragmidium Rubi-saxatilis Liro.

Trail, No. 103 (*P. Rubi* Pers., p.p.); Grove, p. 297 (*P. Rubi* Wint., p.p.).

Moray (Forres).

Aecidiospores.—Sori amphigenous, generally hypophyllous, scattered or grouped, rounded, minute, about $\frac{1}{3}$–$\frac{1}{2}$ mm. in diam. elongated on the nerves, up to 5 mm. long, yellow, surrounded by numerous hyaline, cylindrical paraphyses, rounded at the

apex, 50–75 μ long, 5–8 μ thick; aecidiospores globose, subglobose or ellipsoid, sparsely aculeate, yellow, 18–28 × 16–22 μ, epispore 2–3 μ thick, with 3–7 germ-pores.

Uredospores.—Sori hypophyllous, scattered, minute, rounded, yellow, surrounded by cylindrical-clavate, hyaline paraphyses 50–80 μ long and, at the apex, up to 16 μ wide; pores globose, subglobose, ellipsoid or ovate, sparsely echinulate, yellow, 18–28 × 16–23 μ, epispore $1\frac{1}{2}$–$2\frac{1}{2}$ μ thick, germ-pores indistinct.

Teleutospores.—Sori hypophyllous, scattered or grouped, minute, sometimes confluent, pulverulent, black; spores cylindrical or fusoid-cylindrical 3–7-, generally 5–6-septate, not constricted at the septa, with a hyaline or pale-coloured apical papilla 7–18 μ long, densely verrucose, chestnut-brown, 52–110 × 25–32 μ, epispore 3–4 μ thick, each cell with 2–4 germ-pores; pedicels persistent, hyaline, up to 130 μ long, and up to 11 μ wide in the upper part, dilated up to 18 μ wide near the base.

I, II, III on * *Rubus saxatilis.*

Specimens of this species are included in the Herb. Trail.; they were collected by Keith at Darnaway, Forres, in 1879. It is distinguished from *Phragmidium Rubi* by the larger number of septa in the teleutospore.

164. Phragmidium Rubi-Idaei Kärst.

Trail, No. 106; Grove, p. 298.

Tweed! Forth, Tay! Dee! Moray!

Solway! (Stranraer, New Galloway, Lockerbie), Clyde, Argyle, Ross.

0, I, II, III on *Rubus Idaeus.*

KUHNEOLA Magnus.

165. * Kuhneola albida Magnus.

Grove, p. 300.

Solway (Girvan and Moffat), *Clyde* (West Kilbride and Ayr). *Dee* (Aberdeen).

0, II, III on * *Rubus fruticosus.*

The records for Solway and Clyde were made by the Scottish Cryptogamic Society on their excursions, and that for Aberdeen by Alexander Smith.

166. Kuhneola Tormentillae Arthur.

Trail, No. 101 (*Phragmidium Tormentillae* Fckl.); Grove, p. 301.

Forth.

Clyde.

0, II, III on *Potentilla Tormentilla*.

XENODOCUS Schlecht.

167. Xenodocus carbonarius Schlecht.

Trail, No. 107; Grove, p. 302.

Tweed!

I, III on *Sanguisorba officinalis*.

Recorded from Melrose by M. C. Cooke in 1864 and collected from the same locality in July 1934.

GYMNOSPORANGIUM Hedw. fil.

168. Gymnosporangium clavariaeforme DC.

Trail, No. 109; Grove, p. 304.

Tweed! Forth! Tay! Dee, Moray!

Solway! (Thornhill).

0, I on *Crataegus Oxyacantha*!

III on *Juniperus communis*!

169. Gymnosporangium Juniperi Link.

Trail, No. 110; Grove, p. 307.

Tweed, Forth! Tay! Dee, Moray!

Solway, Clyde, Argyle, Ross!

0, I on *Pyrus Aucuparia*!

III on *Juniperus communis*!

170. Gymnosporangium Sabinae Wint.

Trail, No. 180; Grove, p. 308.

Tweed, *Moray*! (Aviemore).

Clyde (Dalbeth).

I on *Juniperus Sabina*.

[III on *Pyrus communis*.]

The aecidium has not been recorded in Scotland. The record for the Clyde was made by Hopkirk in the Flora Glottiana in 1813 (p. 149), who collected the rust at Dalbeth.

CHRYSOMYXA Unger.

171. Chrysomyxa Empetri Schröt.

Trail, No. 131; Grove, p. 311.

Forth! (Ben Venue), Tay, Dee, *Moray*! (Boat of Garten).

Clyde! (Ben More), *Ross*! (Cape Wrath).

II on *Empetrum nigrum*!

Teleutospores have not been discovered in Great Britain, and the rust is placed in this genus on account of the general structure of its uredospores.

172. * Chrysomyxa Pyrolae Rostr.

Trail, No. 125 (*Melampsora Pyrolae* Gmelin, p.p.); Grove, p. 312.

Tweed! (Berwick), *Forth* (Edinburgh), *Tay* (Dundee), *Dee* (Aberdeen and Kincardineshire), *Moray*! (Beauly and Cullen).

II, III on *Pyrola minor*! and *P. rotundifolia*.

Teleutospore crusts of this rust were found near Cullen, in June 1922, by Alexander Smith. The species has been confused with *Pucciniastrum Pyrolae*, and the records given by Trail under *Melampsora Pyrolae* include both species. The record given for Edinburgh by Grove (p. 312) is probably based on that given in the English Flora (v, pt. 2, p. 378) by Berkeley, which reads: "About Edinburgh, Dr. Greville and Mr. Macnab. Berwick, Dr. Johnston.—*Sporidia* ovate, with sometimes an obsolete peduncle in Mr. Macnab's specimen on *Pyrola rotundifolia*, sori scattered all over the leaf, epidermis ruptured. *Sporidia* in Dr. Greville's specimens on *P. minor* oblong and narrow, sori collected in small clusters." The latter specimens are in the Herb. Edin. and belong to *Pucciniastrum Pyrolae* (see No. 214).

The record for Berwick is from the Herb. Johnston.; that for Aberdeen from Herb. Trail.; for Dundee from the Herb. Edin., collected by William Gardiner in 1845, and for Kincardineshire from specimens collected by Nicholson.

In *Chrysomyxa Pyrolae* the uredospore sori are scattered and often cover the whole leaf, while those of *Pucciniastrum Pyrolae* occur in groups.

173. * Chrysomyxa Rhododendri De Bary.

Grove, p. 384.

Dee (Aberdeen).

Solway! (Stranraer), *Clyde* (Douglas Castle).

0, I on * *Picea excelsa*!

II, III on **Rhododendron hirsutum*.

This rust was first discovered by Boyd, who found the uredospore and teleutospore stages at Douglas Castle in 1913. Shortly afterwards, in October 1913, the aecidial stage was found in the Solway area (Borthwick, Trans. Bot. Soc. Edin., xxvi, 1914, p. xxxiii). An account of the rust was published in 1915 (Borthwick and Wilson, Trans. Roy. Scot. Arbor. Soc., xxix, 1915, p. 187). Specimens of the aecidial stage were collected by Trail in Aberdeenshire in September 1916 (see Grove, J. Bot., lv, 1917, p. 134). The rust may cause serious defoliation of the spruce, but this can only occur in the vicinity of the *Rhododendron*.

174. * **Chrysomyxa Abietis** Unger.

Sydow, Monograph, Ured., iii, p. 519.

Tweed! (Kelso), *Tay* (Loch Tay), *Dee* (Durris, Monymusk, Tarland), *Moray* (Novar).

Solway! (Newcastleton), *Clyde*! (Benmore), *Argyle*! (Inverliever).

III on * *Picea excelsa*! and * *P. sitchensis*!

This rust was first recorded by Somerville from Durris, near Aberdeen, in 1911 (Quart. Journ. For., v, p. 277), and in 1915 (Quart. Journ. For., ix, p. 68) the same author stated that he had received no further records of its occurrence. In 1915 Trail stated: " It is not more than six or seven years ago that I first observed *Chrysomyxa Abietis* in Aberdeenshire, and it is probable that the fungus has only recently made its appearance in the north of Scotland " (Trans. Roy. Scot. Arbor. Soc., xxix, 1915, p. 190, and Notes Roy. Bot. Gard. Edin., ix, 1915, p. 65). In 1915 it was stated to be quite common at Novar in Ross-shire. All the other records were made subsequently to 1920. It appears that the rust is spreading rapidly in Scotland; in England it seems to have been recorded only from Northumberland. It was found on *Picea sitchensis*, a host on which it has not been previously recorded, in April 1934 near Kelso, in the vicinity of infected *P. excelsa*. The sori are frequently attacked by the parasite *Darluca Filum* Cast.

CRONARTIUM Fries.

175. * Cronartium ribicola Fisch. de Waldh.

Grove, p. 316.

Tweed! (Peebles and Stobo), *Tay*! (Murthly), *Moray*! (Beauly and Aviemore).

Solway! (Sandhead), *Clyde*! (Dunoon and Ayr).

0, I on * *Pinus Strobus*! * *P. Cembra*! * *P. monticola*! * *P. excelsa*! * *P. parviflora*! * *P. Ayacahuite*! * *P. Lambertiana*! * *P. flexilis*!

II, III on * *Ribes nigrum*! * *R. rubrum*! * *R. sanguineum*!

This rust was recorded on the various species of *Pinus* in the Trans. Brit. Mycol. Soc., vii, 1921, p. 83, and xii, 1927, p. 114. The aecidial stage is frequently infected by *Tuberculina maxima*.

176. Peridermium Pini Chev.

Trail, No. 127 (*Coleosporium Senecionis* Pers., p.p.).

Tweed! Forth, Tay, *Dee* (Rothiemurchus), Moray!

Spermogonia.—Rather flat, irregular, 2–3 mm. in diameter.

Aecidiospores.—Aecidia erumpent from the bark in the form of a bladder, large, grouped or spread more or less equally over a large part of the branch, 2–7 mm. long, 2–3 mm. wide and high, pseudoperidium minutely verrucose on the exterior, more strongly verrucose on the inner side, firm, consisting of 2–3 layers of cells, provided with stiff hair-like outgrowths from the inner surface which are expanded at the base and up to 1 mm. long, cells of the pseudoperidium up to 70 μ long, 16–36 μ wide, verrucose, with walls 4–6 μ thick; spores globose-ellipsoid or polyhedric, verrucose, 24–31 × 16–23 μ, epispore hyaline, 3–4 μ thick.

0, I on branches of *Pinus sylvestris*!

Trail grouped this rust with *Peridermium acicolum* Link on the needles, and regarded both as the aecidial stage of *Coleosporium Senecionis*. But numerous experimental infections have shown that the *Peridermium* on the branches has no connection with *Coleosporium*.

Stevenson (M.S., No. 1347) separates the two as *P. Pini* Chev. and *P. acicolum* Lk., and the records given (except Dee) are from the Mycologia Scotica. There is a specimen from Rothiemurchus in the Herb. Trail.

P. Pini is now regarded as the aecidial stage of a species of *Cronartium*, but although numerous infection experiments have been made on various plants, no other host has been found. It has been discovered, however, that it is a "repeating" form, *i.e.* the spores will again infect *Pinus sylvestris* (Klebahn, Flora, cxi–cxii, 1923, p. 194).

It is omitted from Grove's British Rust Fungi, although there is little doubt that it occurs in England. There is no reason to believe that *Cronartium flaccidum*, which has been found in England, and which possesses an almost indistinguishable aecidial stage (*P. Cornui* Kleb.) on *P. sylvestris*, occurs in Scotland.

P. pini has been found at Beauly parasitised by *Tuberculina maxima*.

COLEOSPORIUM Lév.

177. Coleosporium Senecionis Fr.

Trail, No. 127 (*Coleosporium Senecionis* Pers., p.p.); Grove, p. 320.

Tweed! (Kelso, Berwick), Forth! Tay! Dee, Moray!

Solway! (Turnberry), Clyde, *Argyle* (Isle of Coll), Ross.

0, I on *Pinus sylvestris*! *P. austriaca*, * *P. Laricio*!

II, III on *Senecio vulgaris*! *S. sylvaticus*! * *S. viscosus*! * *S. Smithii*!

This rust was found on the island of Coll by Symington Grieve in July 1922 on *Senecio Smithii*, a South American species. There are no pines on the island, and the nearest are on the island of Mull, more than ten miles distant. This appears to prove that the rust can exist without the aecidial host; probably by means of uredospores. Aecidiospores from *Pinus sylvestris* placed on *Senecio vulgaris* in June 1929 produced uredospores in about ten days (Trans. Brit. Mycol. Soc., ix, 1924, p. 141).

178. Coleosporium Tussilaginis Kleb.

Trail, No. 128 (2); Grove, p. 322.

Tweed, Forth! Tay, Dee, Moray! Orkney!

Solway! Clyde! Argyle.

0, I on * *Pinus sylvestris*.

II, III on *Tussilago Farfara*!

179. Coleosporium Petasites Lév.

Trail, No. 128 (3); Grove, p. 323.

Tweed! Forth! Tay, Dee, Moray.

Solway! (Creetown), *Clyde*! (Arran, West Kilbride), *Argyle*! (Inverliever), *Ross*! (Skye).

0, I on * *Pinus sylvestris.*

II, III on *Petasites vulgaris*! * *P. japonicus*! * *P. palmatus*!

The records on *P. japonicus* and *P. palmatus* are from Stobo (Trans. Brit. Mycol. Soc., ix, 1924, p. 142).

180. Coleosporium Sonchi Lév.

Trail, No. 128 (1); Grove, p. 324.

Tweed, Forth! Tay, Dee, Moray.

Solway! (Stranraer), Clyde.

0, I on * *Pinus sylvestris.*

II, III on *Sonchus oleraceus*! *S. asper*! *S. arvensis*!

180a. * Coleosporium Cacaliae Fckl.

Grove, p. 325.

Dee (St. Fergus).

[0, I on *Pinus montana* and *P. sylvestris* ?]

II, III on * *Cacalia hastata.*

The uredospore and teleutospore stages of this rust were discovered by Alexander Smith occurring commonly in a garden at St. Fergus. These appear regularly every year although there are no pines within several miles. The stages on *Cacalia* have been found in several places in England, but the aecidial stage has not been found in this country. It is, of course, an introduced species.

181. Coleosporium Euphrasiae Wint.

Trail, No. 130 (*C. Euphrasiae* Schum., p.p.); Grove, p. 236.

Tweed! Forth! Tay, Dee! Moray! *Sutherland*! (Durness).

Solway! (Port William), Clyde! Argyle, *Ross*! (Mallaig).

0, I on * *Pinus sylvestris.*

II, III on *Euphrasia officinalis*! *Bartsia Odontites*! *Rhinanthus Crista-galli*!

182. * Coleosporium Melampyri Karst.

Trail, No. 130 (*C. Euphrasiae* Schum., p.p.); Grove, p. 327.

Tay! (Ballinluig), *Dee*! (Banchory), *Moray*! (Grantown).

0, I on * *Pinus sylvestris.*

II, III on * *Melampyrum pratense*! and its var. * *montanum.*

183. Coleosporium Campanulae Lév.

Trail, No. 129; Grove, p. 328.

Tweed, Forth! Tay! Dee, Moray!

Solway! (Lockerbie), Clyde! Argyle!

0, I on * *Pinus sylvestris.*

II, III on *Campanula rotundifolia*! and cultivated species of *Campanula*!

OCHROSPORA Dietel.

184. * Ochropsora Sorbi Diet.

Trail (*Aecidium leucospermum* DC.) under No. 77 (*Puccinia fusca* Relhan); Grove, p. 329.

Forth! (Edinburgh), *Tay*! (Ballinluig), *Dee* (Corbie Den, Kincardineshire), *Moray.*

Solway, *Clyde* (Gourock), *Argyle.*

0, I on *Anemone nemorosa*!

[II, III on *Pyrus Aucuparia.*]

The uredospore and teleutospore stages have not been found in Britain.

ENDOPHYLLUM Lév.

185. * Endophyllum Sempervivi De Bary.

Grove, p. 335.

Forth (Edinburgh).

0, III on * *Sempervivum tectorum.*

No Scottish specimens of this rust have been seen, but the justification for inclusion rests on a note in Greville's handwriting in his own interleaved copy of the Flora Edinensis which is in the library of the Royal Botanic Garden. The note reads:

"*U. Sempervivi.* Albert. No. 356. *U. ovata* var. Strauss in Annal. Soc. Wetherau. 2. p. 94.

"Hab. on the leaves of *Sempervivum tectorum*, near Edinburgh. Mr. D. Steuart. Deeply immersed in the substance of the leaf, rather large, and somewhat prominent. The epidermis yellow. The clusters or pustules are scattered, very distinct, seldom bursting. Sporules reddish."

MELAMPSORA Cast.

186. * Melampsora Larici-Caprearum Kleb.

Trail, No. 113 (*M. farinosa* Schröt., p.p.) and No. 139 (*Caoma Laricis* Westd., p.p.); Grove, p. 338.

Tweed! (Kelso and Berwick), *Forth*! (Gifford and Fala), *Tay*! (Murthly and Glenalmond), *Moray*! (Grantown).

Solway! (New Galloway), *Clyde*! (West Kilbride and Strachur), *Argyle*! (Taynuilt).

I on *Larix europaea*! * *L. leptolepis*!

II, III on *Salix Caprea*! *S. cinerea*! *S. aurita.*

Teleutospores of this species from *S. Caprea* were placed on the needles of *Larix europaea* in April 1932 and produced the caeoma in ten days. The caeoma was found on *Larix leptolepis* at Benmore, Argyle, in May 1934.

187. * Melampsora Euonymi-Caprearum Kleb.

Grove, p. 339.

Solway! (New Galloway), *Clyde* (Troon).

[0, I on *Euonymus europaeus.*]

II, III on * *Salix cinerea*!

The rust was collected at Troon during the meeting of the Scottish Cryptogamic Society in 1928. The aecidial stage has not been found in Scotland.

188. Melampsora Larici-epitea Kleb. (emend. Fischer).

Trail, No. 114 (*M. epitea* K. et S.) and No. 139 (*Caeoma Laricis* Westd., p.p.); Grove, p. 340.

Tweed! (Innerleithen), *Forth*! (Edinburgh), *Tay* (Perth and Dundee), *Moray*! (Lairg), *Sutherland*! (Tongue).

Clyde! (West Kilbride and Strachur), *Argyle*! (Loch Ailort), *Ross*! (Mallaig).

I on *Larix europaea.*

II, III on * *Salix Caprea*! * *S. cinerea*! * *S. aurita*! *S. viminalis*! * *S. nigricans*! * *S. Smithiana* (*S. mollissima*)! * *S. purpurea*, * *S. hippophaefolia.*

There are specimens on *S. purpurea* in the Herb. Edin. collected by Greville, and also in the Herb. Trail. Greville's specimen in the Herb. Edin. labelled "*Uredo vitellinae* DC. on *Salix mollissima*, Old Botanic Garden," belongs to this species; another specimen of Greville's from Fife labelled *U. vitellinae* is this species on *S. hippophaefolia.*

189. * Melampsora Larici-pentandrae Kleb.

Grove, see note on p. 345.

Tweed (Berwick), *Forth* (Roslin), *Dee* (Aberdeen), *Clyde* (Ayr).

Aecidiospores.—Caeomata bright orange; spores angular-globose or ovate, faintly verruculose, 18–26 × 13–20 μ, epispore 1½–2 μ thick.

Uredospores.—Sori mostly hypophyllous but single ones epiphyllous, up to 1 mm. diam., bright orange; spores ovate, oblong or subclavate, distinctly aculeate, smooth at the apex, 26–44 × 12–16 μ, epispore about 2 μ thick; paraphyses clavate to capitate, 40–60 μ long, up to 22 μ wide above.

Teleutospores.—Sori hypophyllous, subepidermal, scattered or grouped and often covering the whole surface of the leaf, minute, about ·5 mm. in diam., often confluent, yellowish-brown, finally brownish-black; spores prismatic or cylindrical, rounded at both ends, yellowish-brown, 28–38 × 6–11 μ, epispore 1 μ thick.

I on *Larix europaea.*

II, III on * *Salix pentandra.*

Specimens collected by Greville are in the Herb. Edin., others are in the Herb. Trail. and Herb. Johnston. The specimen from Ayrshire was collected by Boyd (see Grove, J. Bot., lix, 1924, p. 314).

190. * Melampsora Ribesii-viminalis Kleb.

Grove, p. 342.

Tay (Dundee).

[0, I on *Ribes Grossularia, R. rubrum, R. nigrum.*]

II, III on * *Salix viminalis.*

There is a specimen of uredospores on *S. viminalis* in the Herb. Edin. *ex herb.* William Gardiner, Dundee, Roscobie, Aug. 1844, which appears to belong to this species.

191. Melampsora Orchidi-repentis Kleb.

Trail, No. 138 (*Caeoma orchidis* A. et S.); Grove, p. 343.

Tay! (Ben Lui and Tentsmoor), *Dee*! (Dess and Cove), *Sutherland*! (Tongue).

Solway! (Sandhead), *Ross*! (Skye).

0, I on * *Orchis incarnata*! *O. maculata, Habenaria* sp.

II, III on *Salix repens*!

The record of the aecidial stage on *Habenaria* from Fern and Monikie by Fergusson (quoted by Stevenson and Trail) may refer to *H. conopsea* or to *H. chlorantha*, both of which are recorded from Forfar and Perth and both recorded on the Continent as host plants by Sydow (Monograph, Uredineae, iii, p. 359). This stage is recorded on *O. maculata* from Cove, near Aberdeen, by Sutherland.

The aecidial stage on *O. incarnata* was found at Tentsmoor, Fife, in June 1932, in close proximity to the uredospore stage on *S. repens*. Plants of *Listera ovata* which were growing close to the infected *Orchis* were not attacked, possibly because they had developed later and were not up at the time of germination of the teleutospores.

Plants of *Salix repens* were found in May 1931 at Tentsmoor bearing uredospores on the leaves, young shoots, and female catkins; the infection of the latter was particularly heavy, the young capsules being covered almost completely by the rust; there were no orchids in the immediate vicinity, and it appears improbable that they had been infected by aecidiospores at this early date. It seems probable that the rust can exist through the winter either as mycelium in the stems or in the uredospore condition.

192. * Melampsora Allii-fragilis Kleb.

Trail, No. 116 (*M. vitellinae* DC., p.p.) and No. 137*a* (*Caeoma Alliorum* Link, p.p.); Grove, p. 344.

0, I on *Allium ursinum*.

II, III on *Salix fragilis*, *S. pentandra*.

In Trail's Revision, the host plants of *M. vitellinae* are stated to be *Salix pentandra*, *S. fragilis*, and *S. vitellina*, and it therefore appears that *M. vitellinae* includes *M. Allii-fragilis* and *M. Allii-Salicis-albae*. *M. vitellinae* is given for all the districts (including Orkney) except Sutherland. It was found at Forres by the Scottish Cryptogamic Society in 1912.

Cooke's specimen of *Caeoma Alliorum* "on *Allium*. Scotland" is the uredospore stage of *Puccinia Porri*. *C. Alliorum* has been recorded for the Clyde district at Seamill (Brit. Assoc. List, 1901), but this may belong to *M. Allii-populina*.

193. * Melampsora Allii-Salicis-albae Kleb.

Trail, No. 116 (*M. vitellinae* DC., p.p.) and No. 137*a* (*Caeoma Alliorum* Link, p.p.); Grove, p. 345.

0, I on *Allium ursinum*.

II, III on *Salix alba* and its var. *S. vitellina*.

Uredo vitellinae is recorded in the Flora Edinenis (p. 437) by Greville on *S. vitellina*, and these records probably refer to *M. Allii-Salicis-albae*.

194. * Melampsora arctica Rostr.

Grove, p. 346.

Tay (Ben an Dothaidh).

II, III on * *Salix herbacea*.

This rust was found by J. H. Wheldon and A. Wilson in 1911 at about 3100 feet on Ben an Dothaidh. When collected the plants bore only uredospores, but they were planted at Walton, near Liverpool, and there after the leaves had fallen two teleutospore sori were developed on them (Annals Scot. Nat. Hist., 1911, p. 37).

As a result of the work of Fraser (Mycologia, iv, 1912, p. 187, and v, 1913, p. 238) *M. arctica* is now known to be a heteroecious species; this investigator infected *Abies balsamea* by sowing upon it teleutospores from *Salix discolor*, this being one of the hosts of the rust. The description of the stage on *A. balsamea* is as follows:—

Spermogonia.—Hypophyllous.

Aecidia.—Caeomata hypophyllous, rather large, orange; spores globose to ovate, faintly verruculose, 15–24 × 13–16 μ, epispore 2–3 μ thick.

There is another species *M. alpina* (*q.v.*, No. 196) of which the uredospores and teleutospores also occur on *S. herbacea*. *M. arctica* appears to differ from *M. alpina* chiefly in the distribution of the sori. The uredospore sori of the former species are described as gregarious, and according to Juel often cover the whole shoot. The infected plants are poorly developed, and it appears that the mycelium is perennial. Both uredospore and teleutospore sori are hypophyllous, while those of *M. alpina* are amphigenous.

M. arctica was previously stated to occur in Switzerland, Greenland, Norway, and Sweden, but later Sydow (Monograph, Uredineae, iii, p. 367) gave Iceland, Greenland, and

Canada as its distribution. *M. alpina* is exclusively European. There appears to have been considerable confusion between the two species, and the Scottish records of *M. arctica* require confirmation.

Search for this species has been carried out without success on a number of Scottish mountains (but not on Ben an Dothaidh).

195. * Melampsora alpina Juel.

Sydow, Monograph, Ured., iii, p. 360.

Tay! (Ben Lawers, Ben Lui).

Clyde! (Ben Bheula, Strachur), *Argyle* (Glen Nevis).

Spermogonia.—Grouped or scattered, 90–130 μ high, 150–160 μ wide, pale orange.

Aecidiospores.—Caeomata epiphyllous or amphigenous, mostly solitary, $\frac{1}{3}$–1 mm. in diam., surrounded by the ruptured epidermis, bright orange; spores globose or ovate, densely verruculose, 16–25 × 14–21 μ, epispore colourless up to 3 μ thick; paraphyses with colourless wall and yellow granular contents, ending in a swollen head which is always smaller than the aecidiospores.

Uredospores.—Sori amphigenous, scattered, minute, rounded, $\frac{1}{4}$–$\frac{3}{4}$ mm. in diam., orange-yellow; spores subglobose, ovate or ellipsoid, finely echinulate-verruculose, 13–21 × 10–16 μ, epispore colourless, up to $1\frac{1}{2}$ mm. thick; paraphyses numerous, capitate, hyaline, up to 88 μ long and 18–24 μ wide in the upper part, wall 3–6 μ thick.

Teleutospores.—Sori amphigenous, rounded, up to ·8 μ in diam., covered by the epidermis, at first brown, then brownish-black; spores prismatic or oblong, rounded at both ends, pale brown, 25–50 × 9–14 μ, epispore 1 μ thick.

I on * *Saxifraga oppositifolia*!

II, III on * *Salix herbacea*!

This species appears to be widely distributed on the higher Scottish mountains (J. Bot., liii, 1914, p. 48, and lvii, 1919, p. 161), but the caeoma has only been found on Ben Lui. It is inconspicuous and easily overlooked; by careful search it could probably be found wherever the saxifrage grows in the vicinity of the infected *Salix*. In several situations the rust has been found on the *Salix* where it is not in the vicinity of the Saxifrage, and there is probably some method by which it can persist without the latter host.

196. * Melampsora reticulatae Blytt.

Sydow, Monograph, Uredineae, iii, p. 362.

Tay! (Ben Lui and Killin), *Dee* (Braemar).

Spermogonia.—Scattered or grouped, 90–125 μ high, about 150 μ wide, pale orange.

Aecidiospores.—Caeomata epiphyllous or amphigenous, solitary or few on each leaf, $\frac{1}{2}$–1 mm. in diam., surrounded by the ruptured epidermis, orange; spores globose, angular-globose to ovate, densely and minutely verruculose, 16–25 × 14–20 μ, epispore 2–3 μ thick.

Uredospores.—Sori hypophyllous, scattered or grouped, rounded, about $\frac{1}{2}$ mm. in diam., bright orange; spores angular-subglobose, ellipsoid, ovate or pyriform, echinuate verrucose all over, 17–27 × 15–19 μ, epispore $2\frac{1}{2}$–$3\frac{1}{2}$ μ thick; paraphyses numerous, capitate, 60–95 μ long, 18–30 μ wide in the upper part, wall up to 10 μ thick.

Teleutospores.—Sori hypophyllous, covered by the epidermis, scattered, minute, $\frac{1}{3}$–$\frac{1}{2}$ mm. in diam., yellow-brown; spores prismatic, rounded at both ends, pale yellow-brown, 35–44 × 10–13 μ, epispore up to 1 μ thick.

0, I on * *Saxifraga aizoides*!

II, III on * *Salix reticulata*.

Specimens of the uredospore and teleutospore stages of this rust are present in the Herb. Trail., collected in Glen Callater, Braemar, in August 1882. Specimens of the uredospore stage were found by Borthwick in Perthshire (Trans. Brit. Mycol. Soc., ix, 1924, p. 139) and Boyd at Killin (Proc. Nat. Hist. Soc. Glasgow, iii, 1889–92, p. xxxv), and recently the caeoma stage has been found on Ben Lui.

197. * Caeoma Saxifragarum DC.

Forth (Ben Venue), *Tay*! (Ben Lui).

0, I on * *Saxifraga hypnoides*!

Spermogonia scattered, rather flat, about ·1 mm. high, ·2 mm. wide. Aecidia scattered on stems and leaves, amphigenous on the latter, surrounded by the ruptured epidermis, ·3–·7 mm. diam.; aecidiospores globose, angular-globose, or ovate, densely and minutely verrucose, 17–20 × 13–20 μ.

The only record of this rust appears to be that given by Dietel in a list of the fungi found in the neighbourhood of Leipzic (Ber. Naturf. Ges. Leipzig, 1890, p. 37). Specimens

collected by Greville on Ben Venue are in the Herb. Edin., and the rust has been found recently on Ben Lui. This is very probably the caeoma stage of some heteroecious species of *Melampsora* of which the other host is a species of *Salix*.

The name *Caeoma Saxifragarum* DC. has also been used for the aecidial stage of the autoecious species *M. vernalis* Niessl., but it is unlikely that the caeoma on *S. hypnoides* belongs to an autoecious species.

198. * Melampsora Allii-populina Kleb.

Trail, No. 118 (*M. populina* Jacq., p.p.) and No. 137*a* (*Caeoma alliorum* Lk., p.p.); Grove, p. 347.

Solway! (New Galloway).

I on *Allium ursinum*.

II, III on * *Populus trichocarpa*.

The aecidial stage on *Allium ursinum* has been recorded from the Clyde area at Seamill (Brit. Assoc. List, 1901), but this may belong to *M. Allii-fragilis* or *M. Allii-Salicis-albae*.

199. * Melampsora Larici-populina Kleb.

Trail, No. 118 (*M. populina* Jacq., p.p.) and No. 139 (*Caeoma Laricis* Plowr., p.p.); Grove, p. 348.

Tweed! (Berwick and Kelso), *Forth*! (Penicuik), *Tay*! (Murthly), *Dee* (Aberdeen), Moray.

Solway! (Carronbridge), *Clyde*! (Arran).

I on *Larix europaea*, * *L. leptolepis*.

II, III on * *Populus trichocarpa*! *P. nigra*! * *P. generosa*! * *P. robusta*! * *P. candicans*! * *P. laurifolia*!

The caeoma on the larch belongs either to this species or to *M. Larici-Caprearum*, *M. Larici-epitea*, *M. Larci-pentandrae*, or *M. Larici-Tremulae*. It has been recorded from Dee and Moray. Recently it has been discovered in the Clyde area on *Larix leptolepis*, a new host for the fungus.

200. Melampsora Larici-Tremulae Kleb.

Trail, No. 117 (*M. tremulae* Tul., p.p.) and No. 139 (*Caeoma Larici* Westd., p.p.); Grove, p. 349.

Forth, Tay! Dee, Moray!

Clyde, *Argyle* (Inveraray).

I on *Larix europaea*.

II, III on *Populus tremula*! *P. alba*!

All these records refer to the uredospore and teleutospore stages, and in these, in the absence of infection experiments, it has not been found possible to distinguish *M. Larici-Tremulae* from *M. Rostrupii*.

Caeoma Laricis has been found in the Clyde, Dee, and Moray districts; at Maidencraig, near Aberdeen, Trail found *C. Laricis* and the stages on *P. tremulae* in close proximity.

201. * Melampsora Rostrupii Wagner.

Trail, No. 117 (*M. tremulae* Tul., p.p.) and No. 137 (*Caeoma Mercurialis* Pers.); Grove, p. 351.

Tweed, Forth! Tay, Dee! Moray.

Clyde (Cumbernauld).

0, I on *Mercurialis perennis*!

II, III on *Populus tremula*! *P. alba*!

Apart from one record in the Forth area, near Gifford, where, in June 1934, heavily infected plants of *Mercurialis perennis* were found immediately underneath aspens which were already infected with the uredospores, all these records refer only to the caeoma on *M. perennis*. All other records of the stages on *P. tremula* and *P. alba* are given under the preceding species (No. 200).

202. Melampsora Euphorbiae Cast.

Trail, No. 111 (*M. Helioscopiae* Wint.); Grove, p. 353.

Forth! Tay, Dee.

Solway! (Gatehouse-of-Fleet).

II, III on *Euphorbia Helioscopia*!

203. Melampsora Hypericorum Wint.

Trail, No. 120; Grove, p. 354.

Tweed! (Peebles), *Tay*! Dee, *Moray*! (Beauly), Orkney.

Clyde! (West Kilbride and Arran), Argyle, *Ross*! (Arisaig).

I, III on *Hypericum perforatum*! *H. pulchrum*! and *H. Androsaemum*!

204. Melampsora Lini Desm.

Trail, No. 112; Grove, p. 355.

Tweed! Forth! Tay, Dee, Moray, *Sutherland*! (Durness), Orkney.

Clyde, *Ross*! (Mallaig and Skye).

II, III on *Linum catharticum*!

205. * Melampsora vernalis Niessl.

Trail, No. 136 (*Caeoma Saxifragae* Strauss, p.p.); Grove, p. 357.

Forth (Edinburgh), *Dee* (Portlethen).

0, I, II, III on *Saxifraga granulata.*

In *C. Saxifragae* Trail also included the rust on *S. aizoides*, which is now known to belong to *M. reticulatae.*

The record for Edinburgh is from Greville, Flora Edin.; that for Dee by Plowright (Trans. Brit. Mycol. Soc., i, p. 59).

MELAMPSORIDIUM Kleb.

206. Melampsoridium betulinum Kleb.

Trail, No. 119 (*Melampsora betulina* Pers.); Grove, p. 358.

Tweed! Forth! Tay! Dee! Moray! *Sutherland*! (Tongue).

Solway! (Lockerbie and New Galloway), Clyde! Argyle! Ross!

0, I on **Larix europaea*! **L. leptolepis*!

II, III on *Betula verrucosa*! and *B. pubescens*!

The stage on the larch was described by Borthwick and Wilson in 1913 (Notes Roy. Bot. Gard. Edin., viii, 1913, p. 79) from Murthly, Perthshire, and Fersit, Inverness. It had previously been recorded by Keith from Rothiemurchus, Inverness (Scot. Nat., vii, 1883–4, p. 271). It has recently been discovered in the Clyde area on *Larix leptolepis*, a new host for the species.

Liro (Acta Societatis pro Fauna et Flora Fennica, xxix, No. 7, 1907, p. 3) in Finland failed to bring about infection of *Larix europaea* and *L. sibirica* with sporidia of *M. betulinum*; he believes that the aecidial stage does not develop in northern regions. He showed that the uredospores will not remain viable during the winter; he also states that the rust persists through the winter in the buds and leaves of infected seedlings, probably in the form of mycelium.

On several occasions extending over a number of years heavily infected seedlings have been removed in autumn to a garden in Edinburgh, but have always failed to reproduce the rust in the following year.

207. * Melampsoridium Alni Diet.

Sydow, Monograph, Ured., iii, p. 430.

Tay! (Tarfside), *Dee*! (Aberdeen).

Clyde (West Kilbride).

[*Spermogonia*.—Amphigenous, mostly hypophyllous, subcuticular, minute, lenticular form, 90–126 × 30–55 μ, honey-yellow; spermatia oblong, 5–9 × 2·4–4·2 μ, smooth, hyaline.

Peridermia.—Hypophyllous, cylindrical, 0·5–2 mm. across, up to 1·4 mm. high; peridial wall colourless, cells quadrilateral or hexagonal in face view, 23·4–36 × 14·4–20 μ, overlapping, inner wall thick, closely verrucose, with uniform papillae; aecidiospores ellipsoidal, 19–26·1 × 15–20 μ; epispore verruculose, 1·8–2 μ thick, with a smooth area on some spores, hyaline; contents orange coloured when the spores are fresh.]

Uredospores.—Sori hypophyllous, producing reddish-yellow spots on the upper surface which are limited by the nerves, scattered or grouped, minute, round, ·2–·4 mm. in diam., orange-yellow, surrounded by a hemispherical peridium which at length opens with a circular pore, peridium firm, made up of minute, polyhaedral smooth cells, 32–56 μ long, which are much elongated around the pore, walls on the outside 1–2 μ thick, on the inside 2–3 μ thick; spores globose, subglobose, ovate or ellipsoid, laxly and shortly echinulate all over the surface, 22–34 × 10–15 μ, epispore hyaline, about 1 μ thick; paraphyses few, rudimentary, fusiform.

Teleutospores.—Sori hypophyllous, covered by the epidermis, scattered or grouped, minute, up to ·5 mm. in diam., at first yellow, then becoming brown or purple-brown, at length blackish-brown; spores oblong, prismatic or clavate, rounded, smooth, yellow, 32–45 × 10–16 μ, epispore about 1 μ thick.

[0, I on *Larix europaea* and other sp.]

II, III on *Alnus glutinosa*! and *A. incana*!

This rust was found in the forest nursery at Craibstone, Aberdeen, on two-year seedlings (Trans. Brit. Mycol. Soc., lx, 1921, p. 140). It had previously been described from Aberdeen by Farquharson (Annals Scot. Nat. Hist., 1911, p. 240), and was collected by Boyd in Ayrshire (see Grove, Journ. Bot., lix, 1921, p. 315); recently it was found at Tarfside on bushes of *A. glutinosa*. Hiratsuka, who has

recently investigated the species of *Melampsoridium* on *Alnus* in Japan (Journ. Faculty Agric. Hokkaido Imp. Univ., xxi, pt. i, 1927, and Jap. Journ. Bot., vi, 1932, p. 1) considers that the Craibstone specimens show a very close affinity with *M. Hiratsukanum* Sto. which has its aecidial stage on *Larix Kaempferi*, *L. europaea*, and *L. dahurica* var. *japonica*.

This aecidial stage is similar to that of *M. alni*, which has been described on the same hosts. *M. Hiratsukanum* possesses smaller uredospores which are echinulate over the whole surface, while those of *M. alni* have a smooth spot at the apex; the ostiolar cells of the pseudoperidium of the uredospore sorus of the latter species are short, while in *M. Hiratsukanum* they are much elongated.

The aecidial stage of the Scottish rust has not been found.

MELAMPSORELLA Schröt.

208. Melampsorella Caryophyllacearum Schröt.

Trail, No. 126 (*M. Cerastii* Pers.); Grove, p. 360.

Tweed! Forth, Tay! Dee, Moray!

Solway! (Thornhill and Girvan), *Clyde*! (Dunure and Strachur), *Argyle*! (Fort William and Taynuilt).

0, I on * *Abies pectinata*! * *A. Nordmanniana*!

II, III on *Cerastium arvense*, * *C. triviale*! * *C. arcticum*, * *C. semidecandrum*, * *Stellaria Holostea*! *S. graminea*!

Abies Nordmanniana, *Cerastium arcticum*, *C. semidecandrum*, and *Stellaria Holostea* are new British hosts for this rust.

It has been found on *C. arcticum* at about 3000 feet on Ben Nevis and on *C. semidecandrum* on salt marshes at Tentsmoor, Fife, and in both these localities no silver firs were present within a considerable distance. The rust is known to possess a perennial mycelium in the teleutospore host, and it appears that the aecidial host is not necessary for its continued existence. Uredospores are usually produced in great abundance and are often found on the sepals as well as on the leaves.

209. Melampsorella Symphyti Bubák.

Trail, No. 133 (*Uredo Symphyti* DC.); Grove, p. 363.

Forth!

Clyde! (Milngavie).

(0, I on *Abies pectinata*).

II, III on *Symphytum officinale* and * *S. tuberosum*!

This was found on *S. officinale* near Dunfermline, by Trail in 1889 in the uredospore condition (Scot. Nat., 3rd ser., i, 1891, p. 31), and it has occurred for many years on *S. tuberosum* in the Royal Botanic Garden, Edinburgh; it was found by K. W. Braid at Milngavie in 1834.

Teleutospores have recently been discovered on *S. peregrinum* in England (Trans. Brit. Mycol. Soc., xviii, 1934, p. 274).

PUCCINIASTRUM Otth.

210. Pucciniastrum Agrimoniae Tranzschel.

Trail, No. 132 (*Uredo Agrimoniae* DC.); Grove, p. 364.

Tweed.

Solway! (Gatehouse-of-Fleet).

II, III on *Agrimonia Eupatoria*!

This rust has only been recorded twice from Scotland, and each time from the extreme south. It is said to be common in England. The host plant is not uncommon in Scotland and extends north to Sutherland, but it appears that the rust is confined to the south. Only the uredospore stage has been discovered in Britain.

211. Pucciniastrum Circaeae Speg.

Trail, No. 122 (*M. Circaeae* Schum.); Grove, p. 365.

Tweed! (Earlston), Forth! Tay, Dee, *Moray*! (Beauly).

Solway (Lockerbie and Thornhill), Clyde! *Argyle*! (Ford), *Ross*! (Mallaig).

II, III on *Circaea lutetiana* and *C. intermedia*.

The teleutospore stage has not been found in Scotland.

212. Pucciniastrum Abieti-Chamaenerii Kleb.

Trail, No. 121 (*Melampsora pustulata* Pers., p.p.); Grove, p. 366 (*P. pustulatum* Dietel, p.p.).

Tweed! (Kelso), *Forth*! (Edinburgh).

Clyde (Glasgow).

[0, I on *Abies pectinata*.]

II, III on *Epilobium angustifolium*!

The aecidial stage has not been found in Britain.

213. * Pucciniastrum Epilobii Otth.

Trail, No. 121 (*Melampsora pustulata* Pers., p.p.); Grove, p. 366 (*P. pustulatum* Dietel, p.p.).

Forth (Edinburgh), *Tay*! *Sutherland*! (Ben Loyal).

Clyde (Islay).

Uredospores.—Sori hypophyllous, later also epiphyllous, generally seated on yellow or reddish spots, often on the stems, scattered or in groups, minute, rounded, ·1–·25 mm. in diam., surrounded by the peridium and ruptured epidermis, at length opening with a central pore and then pulverulent, orange-yellow; peridium hemispherical, rather thin, made up of minute, cubical, smooth thin-walled cells (wall about 2 μ thick), 10–18 μ long, cells near the ostiole rather thicker walled (2–3 μ thick); uredospores ovate or ellipsoid, remotely and shortly echinulate, $15-23\times10-15$ μ, with hyaline epispore 1 μ thick.

[*Teleutospores*.—Sori hypophyllous, rarely epiphyllous or on the stems, subepidermal, very minute, ·1–·2 mm. in diam., mostly in groups, pale brown, slightly raised; teleutospores intercellular, oblong to spherical, becoming angular, 2–4-celled, smooth, brown, 2-celled $18–28\times7–15$ μ, 4-celled 20–30 μ in diam., epispore 1–1½ μ, 2–3 thick at the apex.]

II, III on **Epilobium alpinum*! **E. palustre*.

This species was found on Meall nan Tarmachan in Perthshire at about 3000 feet by Matthews on *E. alpinum* in June 1922. It was grown on at Edinburgh for several months, but produced only uredospores. These showed up very conspicuously on the bright green leaves, especially after the dehiscence of the sori. The spores were produced in great abundance and fell to the ground in powdery masses. No spots were produced on the leaves. Other plants of *E. alpinum* were readily infected, but all attempts to infect *E. angustifolium*, *E. obscurum*, *E. montanum*, and *E. alsinaefolium* resulted in failure. The species is, however, recorded by Sydow (Monograph, Uredineae, iii, p. 444) on the last two species. It appears therefore that a specialised form exists on *E. alpinum*.

This species was also found on the same host on Ben Loyal in 1931 at about 2300 feet. Greville has recorded *Uredo pustulata* on *E. palustre* in the Flora Edin. (p. 441), and this probably refers to this rust. The records of *P. pustulatum*

on *E. palustre* from Pitlochry in the report of the Scottish Cryptogamic Society for 1906 and by Boyd from Islay (Glasgow Nat., viii, 1905–8, p. 121) also probably refer to this species.

The teleutospore stage has not been found in Scotland.

Faull (Proc. Inter. Congress Pl. Sci. Ithaca, ii, p. 1743), in North America, has shown by infection experiments that this species produces a peridermial stage on *Abies balsamea*.

214. Pucciniastrum Pyrolae Schröt.

Trail, No. 125 (*Melampsora Pyrolae* Gmel., p.p.); Grove, p. 367.

Forth (Edinburgh, Queensferry, and Loch Leven Island), *Tay*! (Ballinluig).

II, III on *Pyrola minor*! and *P. media*.

This was confused with *Chrysomyxa Pyrolae* by Greville and Trail. The specimens from Ravelrig Toll (Edinburgh) and Queensferry referred to in Greville's Flora Edin. are in the Herb. Edin. Those from Loch Leven are in the Herb. Trail. The teleutospore stage has not been found in Scotland.

For distinctions between this species and *Chrysomyxa Pyrolae*, see No. 172.

215. Pucciniastrum Goodyerae Tranzsch.

Sydow, Monograph, Uredineæ, iii, p. 456.

Moray! (Beauly and Cullen).

II on *Goodyera repens*!

This was mentioned by Grove under *Melampsora Orchidi-repentis*, but there seems to be no doubt that it is *P. Goodyerae* described by Tranzschel and Arthur (N. Am. Flora, vii, p. 105). The aecidial and teleutospore stages are unknown.

THECOPSORA Magnus.

216. Thecopsora areolata Magn.

Trail, No. 123 (*Melampsora Padi* K. et S.) and No. 145 (*Aecidium strobilinum* A. et S.); Grove, p. 368 (*T. Padi* Grove).

Tweed! *Forth* (Edinburgh), Tay! Dee, Moray!

Solway (Dumfries), Clyde, Argyle.

0, I on cone scales of *Picea excelsa*!

II, III on *Prunus Padus*!

In the British Museum Herbarium there are two specimens of the aecidial stage collected by M. C. Cooke near Edinburgh, and also one collected by A. Lorrain Smith in Dumfriesshire.

217. * Thecopsora Galii De Toni.

Grove, p. 370.

Solway (Dumfries), *Clyde* (West Kilbride).

II, III on * *Galium verum*, * *G. saxatile* and * *Asperula odorata*.

The only Scottish specimens known are those discovered by Boyd (see Scot. Crypt. Soc. Rpt., 1921, and Grove, Journ. Bot., lix, 1921, p. 314).

218. Thecopsora Vacciniorum Karst.

Trail, No. 124 (*Melampsora Vacciniorum* Link); Grove, p. 371.

Tweed, Forth, Tay! Dee! Moray! Orkney.

Solway (Thornhill and Girvan), Clyde! Argyle, *Ross*! (Kintail).

II, III on *Vaccinium Myrtillus*! *V. Vitis-Idaea* and *V. uliginosum*!

This rust was discovered by Trail on the three species of *Vaccinium*. Specimens on *V. Vitis-Idaea* are in the Herb. Trail., collected by Keith at Grantown in August 1880; these show very decided yellow spots on both surfaces of the leaf. Specimens showing a heavy infection on *V. uliginosum* were collected on Ben Lui in September 1921.

The teleutospore stage has not been found in Scotland.

In North America the aecidial stage, *Peridermium Peckii* Thum. has been shown by infection experiments to occur on *Tsuga canadensis* (Arthur, N. Am. Fl., vii, p. 678).

CALYPTOSPORA J. Kühn.

219. * Calyptospora Goeppertiana Kühn.

Grove, p. 372.

I on * *Abies pectinata*, * *A. Nordmanniana*.

III on * *Vaccinium Vitis-Idaea*.

The inclusion of this as a Scottish species rests on the statement made by Grove (British Rust Fungi, p. 372) that it has been found in Scotland. There are no British specimens

in the Herb. Kew., the Herbarium of the British Museum, or in any of the Scottish herbaria. Its occurrence in Scotland requires confirmation.

HYALOPSORA Magnus.

Heteroecious or aecidia unknown.

Teleutospores in one or two layers, produced in the epidermal cells which are united into crusts; spores with colourless membrane, each divided by vertical septa into 2–4 (or more) cells. Uredo-sori subepidermal, without a peridium or with a very rudimentary one, but surrounded by paraphyses; uredospores of two kinds, yellow, sessile, furnished with evident germ-pores. Aecidia bladder-like; aecidiospores verrucose with thin colourless wall. Spermogonia conspicuous, yellow, oval in section, subepidermal.

On Ferns with the aecidial stage as far as known on *Abies* sp.

220. * Hyalopsora Aspidiotus Magn.

Trail, No. 134 (*Uredo Polypodii* Pers., p.p.); Grove, p. 374.

Dee (Braemar).

[Spermogonia hypophyllous, alternating irregularly with aecia in two rows, one on each side of midrib, forming conspicuous round yellow spots on the under surface. In section of leaf conspicuous, oval, subepidermal, 400–500 μ long by 90–120 μ deep. Aecidia from mycelium freely distributed through mesophyll, hypophyllous in two rows, one on each side of midrib, bladder-like, spherical, low, 0·4–0·5 mm. in diameter and often only 0·2 mm. high; peridium colourless, delicate, rupturing at apex, cells oblong, 15–20 × 18–32 μ, walls thick, 2–3 μ; aecidiospores globoid or broadly ellipsoid, 13–18 × 15–25 μ, yellow; wall colourless, thin, verrucose.]

Uredospores.—Sori amphigenous, scattered, small, round, up to ·5 mm., golden-yellow, without a peridium, dehiscing irregularly, often seated on yellowish spots; spores oblong or ellipsoid, of two kinds: (1) thick-walled ($2\frac{1}{2}$–$3\frac{1}{2}$ μ), with very faint, hardly perceptible warts, 36–72 × 30–40 μ, with 6–8 scattered germ-pores; (2) thin-walled (about $1\frac{1}{2}$ μ), covered uniformly with very faint scattered warts, 28–40 × 16–26 μ, with four indistinct equatorial germ-pores; paraphyses few, cylindrical or clavate, thin-walled, hyaline.

Teleutospores.—In the epidermal cells, often filling them

completely, roundish or irregular, flattened where they are in contact, sometimes arranged in two layers, about 25 μ high, 21–35 μ or more wide, divided by vertical septa into 3–5 (mostly 4) cells; epispore thin, smooth, colourless; germ-pore not perceptible.

[0, I on *Abies pectinata*, on leaves of third previous season, *i.e.* the collections of 1922 occurred on the needles of 1920.]

II, III on *Polypodium Dryopteris*.

The aecidial stage on *A. balsamea*, known as *Peridermium pycnoconspicium*, has been described by Bell (Bot. Gaz., lxxvii, 1924, p. 1) in North America, and the relationship has been proved by Faull (Proc. Inter. Congress Pl. Sci. Ithaca, 1926, p. 1735) by infection experiments. It has not been found in Britain, but occurs in Switzerland on *A. pectinata*.

There is a specimen in the Herb. Edin. ex herb. William Gardiner from Craig Nich (Angus ?), July 1845, and also one in the Herb. Trail., collected at Braemar in August 1882.

221. * Hyalopsora Polypodii Magn.

Tay (Ben Lawers), *Dee* (Aberdeen).

II, III on *Cystopteris fragilis*.

There is a specimen in the Herb. Edin. collected by Greville on Ben Lawers in 1823, and the record by Buchanan White is from the same locality (Scot. Nat., iv, 1877, p. 27). In the Herb. Trail. is a specimen on *C. fragilis* grown in a greenhouse at Aberdeen. The aecidial stage is unknown.

MILESINA P. Magn.

Heteroecious. Teleutospores within the epidermal cells, 2-multicellular, smooth, hyaline. Uredo-sori furnished with a peridium which opens at the summit with a pore; uredospores hyaline, pedicellate, with a thin epispore, but without germ-pores.

Aecidia from a limited mycelium, not changing the form of the leaf, white, deep-seated, cylindrical; pseudo-peridium colourless, opening at the apex and becoming lacerate; aecidiospores verrucose with colourless contents.

Spermogonia irregularly scattered, small, inconspicuous, extended both above and below the epidermis, in section hemispherical to spherical.

On *Abies* sp. and ferns.

222. * **Milesina Kriegeriana** P. Magn.

Sydow, Monograph, Uredineae, iii, p. 390.

Tweed! (Kelso), *Forth*! (Balcarres), *Tay*! (Dunkeld), *Moray*! (Dochfour and Banff).

Clyde! (Benmore), *Argyle*! (Inverliever).

Spermogonia.—Few, scattered punctiform, inconspicuous, honey-yellow, small, extended both above and below epidermis, hemispherical in section, 100–130 μ broad, 40–50 μ high.

Aecidiospores.—Arising from a limited mycelium, not changing the form of the leaf but causing it to become pale green or whitish, hypophyllous in two irregular rows on yellowish spots occupying a part or all of a leaf, white even before spores are discharged, deep-seated, cylindrical, or somewhat flattened laterally, rather small, 0·2–0·5 mm. across, opening at apex; peridium colourless, margin erect, erose or somewhat lacerate, cells overlapping, with medium thick walls 2–4 μ, the outer smooth, inner somewhat thicker and rather coarsely verrucose; aecidiospores broadly ellipsoid or globoid 18–22 by 20–30 μ, wall thin 1–1·5 μ, densely and rather coarsely verrucose; contents colourless.

Uredospores.—Sori hypophyllous, scattered, at first covered by the epidermis, minute, 1 mm. in diam., rounded, yellow, surrounded by the peridium which at length opens at the apex; spores ovate or ellipsoid, sparsely verruculose or echinulate, hyaline, 25–34 × 16–22 μ, epispore 1–1·5 μ thick.

Teleutospores.—Sori hypophyllous, produced in the epidermal cells, densely crowded, longitudinally septate, 2–8-celled, smooth, hyaline, 14–18 μ high, 14–16 μ wide, epispore 1 μ thick.

0, I on * *Abies pectinata*! * *A. Nordmanniana*! and * *A. cephalonica*!

II, III on * *Aspidium dilatatum*! * *A. Filix-mas*! and * *A. spinulosum*.

This species was first discovered on the fern by Boyd (see Grove, J. Bot., lix, 1921, p. 109) in Ayrshire; it is widely distributed in Scotland, being most commonly found on *A. dilatatum*.

The aecidial stage on *Abies pectinata* (known as *Aecidium pseudo-columnare*) was first discovered in 1924 at Dochfour, Inverness (Trans. Brit. Mycol. Soc., ix, 1924, p. 142); it has

since been found in Argyleshire and at Kelso. Since, however, it is now known that other species of *Milesina* produce similar aecidia on *Abies pectinata* it is possible that all the records do not refer to *M. Kriegeriana*.

Conspicuous blackening of the fern leaves is produced by this rust. The uredospore stage may be found at any time during the year, and there is no doubt that the rust may persist in this form throughout the winter.

Teleutospores were first found on *A. dilatatum* at Kelso in May 1932. The sori are very inconspicuous and give a grayish appearance to the blackened areas; they occur most commonly on the leaves of young plants which do not bear sporangia and which persist in a green condition through the winter. They have been found more abundantly on *A. dilatatum* than on *A. Filix-mas*. Germination and the production of promycelia takes place quite readily in April or May.

223. * Milesina Polystichi Grove.

Grove, J. Bot., lix, 1929, p. 109.

Clyde (West Kilbride).

Uredospores.—Sori hypophyllous, scattered, bullate, roundish ·2–·3 mm. across, prominent; pseudo-peridium hemispheric, firm; pseudoperial cells colourless, elongate at sides, about 21 μ long, polygonal above, about 7 μ across, the walls 2·5 μ thick; spores obovoid or oblong, 18–23 × 26–35 μ; wall colourless, moderately thick 1·5–2·5 μ, strongly and very sparsely echinulate.

II on * *Polystichum angulare*.

This was discovered by Boyd in 1921 (see Grove, J. Bot., lix, 1921, p. 109). It has been suggested that, in North America, the aecidium of this rust is *Peridermium rugosum* which occurs on *Abies amabilis* and *A. grandis* (Hotson, Prel. List of Uredinales of Washington, Pub. Puget Sound Biol. Sta. Univ. Wash., iv, 1925, p. 293, and Boyce, Phytopath., xviii, 1928, p. 705); this occurs on the needles of the current year.

224. * Milesina murariae Grove.

Grove, J. Bot., lix, 1921, p. 311.

Forth! (North Berwick).

Clyde (Dundonald), *Argyle* (Inveraray).

Uredospores.—Sori hypophyllous, covered by epidermis, small, inconspicuous, whitish, bullate, collected on yellowish fading spots of the leaf, often surrounded by a delicate at length wide-open peridium, composed of more or less isodiametric translucent pale-coloured cells, which become elongated round the orifice and paler. Uredospores variable, roundish, ellipsoid, oval or obovoid, 30–45 × 20–24 μ; membrane colourless, 1·5–2 μ thick, at first quite smooth, at length marked with rather few distant, irregular, not prominent warts; contents very granular, colourless; no germ-pores; each spore seated at first (when young) by a truncate base on a supporting cell. The sorus is surrounded by 1–3 rows of clavate, hyaline, pedicellate paraphyses.

II on living leaves of * *Asplenium Ruta-muraria*!

This was first discovered by the Scottish Cryptogamic Society at Inveraray in 1907. It was found by Boyd in 1921 at Dundonald (see Grove, J. Bot., lix, 1921, p. 311) and was found at North Berwick in 1932. No teleutospores have been yet discovered.

225. * Milesina Blechni P. Magn.

Trail, No. 135 (*Uredo Scolopendrii* Fckl., p.p.); Grove, p. 377.

Tay (Pitlochry), *Moray*! (Beauly, Aviemore, and Banff), *Sutherland*! (Tongue).

Solway! (Girvan, Stranraer, New Galloway), *Clyde*! (Benmore and West Kilbride), *Argyle*! (Taynuilt), *Ross*! (Mallaig).

Spermogonia.— } As in *M. Kriegeriana*, No. 222.
Aecidiospores.— }

Uredospores.—Grove, p. 377.

Teleutospores.—Produced in the cells of the lower epidermis, usually densely aggregated, ovate or ellipsoid, 1–4-celled, smooth, hyaline, 11–20 μ high, 12–23 μ wide, epispore 1 μ thick.

0, I on *Abies pectinata*.

II, III on *Blechnum Spicant*!

Widely distributed in Scotland. Uredospores may be found all the year round, and the rust can evidently persist through the winter in this condition. The teleutospores may be found on the discoloured areas of leaves which have persisted in a green condition through the winter. Such leaves

are borne especially on young plants which have not yet produced the fertile leaves. The teleutospores germinate readily in April or May.

226. * Milesina Dieteliana P. Magn.

Trail, No. 136 (*Uredo Scolopendrii* Fckl., p.p.); Grove, p. 376.

Tay! (Glenalmond), *Dee* (Forfarshire ?), *Moray*! (Beauly).

Solway! (New Galloway), *Clyde*! (Benmore and Arran), *Argyle* (Inveraray and Mull).

Spermogonia.— } As in *M. Kriegeriana* ?
Aecidiospores.— }

Uredospores.—Sori hypophyllous, small, round, pustular, clustered loosely in small groups on brown irregular spots, pale brown; spores colourless, oblong or ovate, strongly but sparsely and irregularly echinulate above, smooth below, 22–30 × 15–16 μ; wall moderately thick (1·5–2 μ).

Teleutospores.—Sori produced in the cells of the lower epidermis, solitary or often grouped, 2–4-celled, smooth, hyaline, 12–30 μ high, 12–25 μ wide, epispore 1 μ thick.

II, III on *Polypodium vulgare* and its var. *serratum*.

This rust is widely distributed in Scotland and is often quite obvious on account of the brown spotting of the leaves of the host. The uredospores may be produced all the year round, and there is no doubt that the rust persists in this manner through the winter.

Up to the present teleutospores have not been recorded in Britain, but they were found in two localities in the spring of 1932. There appears to be no external sign of their presence, and they were only found by the microscopic examination of the stripped-off epidermis.

Apparently no infection experiments have been carried out with this species, and in consequence the aecidial stage is unknown. It is, however, very probable that it resembles that of the allied species. Since teleutospores are now known to occur it is possible that some of the specimens of *Aecidium pseudo-columnare* belong to this species.

227. * Milesina Scolopendrii Jaap.

Grove, p. 378 (*Uredo Scolopendrii* Schröt.).

Clyde! (Arran and Benmore).

Uredospores.—Sori hypophyllous, seated upon minute

orbicular yellow or yellowish-brown spots ·5–2 cm. wide, scattered or loosely grouped, minute, rounded, ·1–25 mm. in diameter, yellow, surrounded by a thin peridium; spores very numerous, oozing out, ellipsoid, ovate or often oblong, strongly echinulate all over, hyaline, 28–50 × 15–20 μ, epispore 2 μ thick.

Teleutospores.—Sori hypophyllous, often covering the whole surface of the leaves, whitish yellow or pale yellow, intracellular; teleutospores in the epidermal cells, solitary or grouped, ellipsoid or somewhat polygonal, divided into 2 to 4 cells, 19·8–37·8 × 18·0–27·0 μ; epispore hyaline, smooth.

II, III on * *Scolopendrium vulgare*!

This has been found in considerable abundance in two localities, in Arran in April 1933 by Miss Lauder Thomson, and at Benmore in May 1934. In both cases uredospores and teleutospores were present on the under surface of the leaves of the previous year, borne on large brownish irregular areas. The rust occurs most frequently on leaves which have not produced sporangia, especially on young plants.

Teleutospores occurred in abundance, but their presence could only be determined by microscopic examination. Germination took place readily on keeping the leaves in a damp atmosphere in the laboratory.

Grove recorded this as a Scottish rust (Brit. Rust Fungi, p. 378, and Journ. Bot., lix, 1921, p. 109) apparently on account of the specimens referred to by Buchanan White (Scot. Nat., iv, 1877, p. 27), but these are stated to have been received from North Wales.

In the reference in the Gardener's Chronicle (xii, 1892, p. 776) the origin of the specimens is not stated, but they appear to have come from England.

The teleutospores were first found by Hiratsuka in Japan in 1927 (Jap. Journ. Bot., iii, 1927, p. 289), and there appears to be no other record of their occurrence. The aecidial stage is unknown, but from a consideration of the life-history of allied species it is probably a *Peridermium* on *Abies* sp.

UREDINOPSIS P. Magn.

Heteroecious.

Teleutospores solitary, extracellular in the mesophyll, hyaline, septate. Uredo sori subepidermal with a distinct

peridium, dehiscent by a central pore; uredospores of two kinds, hyaline, pedicellate, without germ-pores. Spermogonia subcuticular, hemispheric, yellow. Aecidia shortly cylindrical or laterally compressed, pseudo-peridium membranous dehiscing at the apex; aecidiospores globose or ellipsoid, colourless, verrucose.

On *Abies* sp. and ferns.

228. Uredinopsis filicina Magn.

Grove, p. 379.

Clyde! (Strachur).

II, III on *Polypodium Phegopteris*.

This is the first record of this species in Great Britain; it was collected in July and September 1929 near Strachur, where it occurred in abundance. Its life-history has not been worked out, but, judging from the investigations on several American species, it is probably heteroecious with its aecidial stage on *Abies*.

The account given of the spermogonia and aecidia in the description of the genus has been taken from the investigations carried out on American species.

The specimens collected in July possess numerous sori containing the thin-walled fusiform uredospores which emerge from the sori in an obvious white tendril. Those collected in September bear numerous sori of the thick-walled stalked uredospores, and also the teleutospores embedded in the mesophyll.

UREDO Pers.

229. * Uredo Lynchii Plowr.

Grove, p. 385.

Clyde (Glasgow).

II * *Spiranthes* sp.

This species was found on *Spiranthes* sp. in a greenhouse at Glasgow by Boyd. It is an imported species.

230. * Uredo anthoxanthina Bubák.

Grove, p. 269 (*Puccinia Anthoxanthi* Fckl., p.p.).

Tweed! (Peebles), *Forth*! (Ben Voirlich), *Tay*! (Ballinluig), *Dee*! (Aberdeen), *Sutherland*! (Ben Loyal).

Solway! (Sandhead), Clyde! (Ayrshire and Arran), Argyle! (Skye), *Ross*! (Mallaig).

II on * *Anthoxanthum odoratum*!

This rust was first collected on Ben Voirlich (Loch Lomond) in 1915. It was suggested (J. Bot., liii, 1915, p. 47) that in Britain two rusts had been confused under the name *Puccinia Anthoxanthi* Fckl.; in 1921 Grove (J. Bot., lix, 1921, p. 312) stated that this was the case and described the occurrence of *U. anthoxanthina*, a species described by Bubák in 1905, as well as *P. Anthoxanthi* Fckl. *U. anthoxanthina* was recorded from Perthshire in 1921 as *P. Anthoxanthi* (Trans. Brit. Mycol. Soc., vii, 1921, p. 83), and additional localities and further particulars were given in 1924 (Ibid., ix, 1924, p. 138).

It is distinguished from the uredospore stage of *P. Anthoxanthi* by its brighter orange colour and by the presence of numerous capitate paraphyses. The sori may be found sometimes on the stem and inflorescence. Sori have been found in March on plants which appeared to be uninfected in the previous autumn, and it is possible that the rust persists through the winter as mycelium in the leaf.

The species is often found at high altitudes.

231. * Uredo ammophilina Kleb.

Sydow, Monograph, iv, p. 528.

Forth! (North Berwick, Kincraig Links and Burntisland), *Dee*! (Aberdeen), *Moray*! (Lossiemouth), *Sutherland*! (Durness).

Solway! (Sandhead), *Clyde*! (Arran), *Ross*! (Mallaig).

Uredospores.—Sori scattered in short series in the grooves of the upper surface of the leaf, producing yellow spots on the under surface, at first covered by the inflated epidermis, then naked, orange; spores oval, 27–29 × 21–26 μ, membrane pale yellow or colourless, 1·5 μ thick, echinulate (distance between spines 1·5–2 μ), with about 9 scattered germ-pores; paraphyses capitate 65–90 × 14–21 μ with a pale yellowish membrane, scattered through the spore layer or rarely absent.

II on * *Ammophila arundinacea*!

Not previously recorded in Scotland, but recorded from Wales by Grove (J. Bot., xlix, 1921, p. 313), and also found in Cumberland. An unnamed specimen, collected at Kingcraig Links, Fife, in August 1889, is preserved in the Herb. Trail.

Occasionally there is a very heavy infection by this rust, and when this occurs the whole leaf becomes pale yellow and is flatter than the normal incurved leaves. A very similar fungus, *Uredo Ammophilae* Syd. (Sydow, Monograph, iv, p. 528), has been described by Sydow from the Isle of Rugen. This possesses uredospores with thicker walls (up to 6 μ) and more distant spines; both species occur on the upper surface of the leaf. No sign of teleutospores belonging to *U. ammophilina* has been found, even on the dead leaves.

232. * Uredo Airae Lagh.

Sydow, Monograph, iv, p. 599.

Forth! (Edinburgh, Pathhead, Aberlady), *Tay*! (Ballinluig). *Solway*! (Thornhill, New Galloway), *Clyde*! (Strachur), *Ross*! (Mallaig).

Uredospores.—Sori generally epiphyllous, often on yellowish or violet spots, scattered or in short rows, elliptic or oblong, ·25–·75 mm. long, rather long covered, yellow; spores almost spherical, ovoid or ellipsoid, densely verrucose or warted, 24–32 × 18–26 μ, membrane hyaline or almost hyaline, 1·5 μ thick with 6–8 scattered germ-pores; paraphyses numerous, club-shaped or capitate, mostly hyaline, finally brownish, 60–90 × 10–18 μ, wall at the apex 2–4 μ thick.

II on * *Aira caespitosa*!

This species is mentioned by Grove (Brit. Ured., p. 265) under *P. dispersa*. It was first recorded from Scotland in 1921 (Trans. Brit. Mycol. Soc., vii, 1921, p. 82). Cruchet and Mayor (Bull. Soc. Vau. Sc. Nat., li, 1917, p. 628) have reported the discovery of teleutospores and state that it is the uredospore stage of *Puccinia Aerae* Cruch. et Mayor.

233. * Uredo Glyceriae Lind.

Sydow, Monograph, iv, p. 540.

Forth! (Linlithgow).

Uredospores.—Sori epiphyllous, few, rounded elliptic or elongated up to 1 mm. long, surrounded by the ruptured epidermis, yellow; spores globose, ovoid or ellipsoid, verrucose-echinulate, subhyaline or yellow, 24–30 × 20–25 μ, epispore 1–1·5 μ thick, with 8–10 scattered germ-pores; paraphyses usually abundant, clavate or capitate, 50–65 μ long, 14–16 μ wide at the apex, hyaline or pale yellow above, wall about 2 μ thick.

II on * *Glyceria maritima*!

This was collected near Linlithgow by Dr. M. M. B. Knagg in May 1925 (Trans. Brit. Mycol. Soc., xii, 1927, p. 115). This is the only British record.

234. * Uredo Festucae DC.

Sydow, Monograph, iv, p. 539.

Tweed! (Berwick), *Forth*! (North Berwick), *Moray*! (Huntly).

Solway! (Dalry), *Clyde*! (Carnwath), *Argyle*! (Taynuilt), *Ross*! (Morar).

Uredospores.—Sori epiphyllous, buried in leaf, the tissue around each sorus conspicuously yellowed and giving rise at first to a yellow band in the leaf which later becomes brown; spores nearly spherical, sometimes broadly ovoid, echinulate or covered with stumpy points, wall brownish yellow 1·5 μ thick, germ-pores 4–6. Paraphyses absent.

II on **Festuca ovina*!

This species was recorded in England by Grove on *Festuca ovina*, *F. rubra*, and *F. duriuscula* (J. Bot., lix, 1921, p. 314), but has not been previously described from Scotland. The yellow bands in the leaf are up to 4 mm. across; they are usually few but are sometimes fairly numerous, and then the leaf shows alternating bands of yellow discoloured tissue and green normal tissue.

AECIDIUM Pers.

235. Aecidium Ranunculacearum DC. var. **Linguae.**

Trail, No. 144; Grove, p. 387.

Forth.

I on *Ranunculus Lingua.*

This was discovered by Greville at Duddingston Loch, Edinburgh, in 1821, but does not appear to have been found since. *R. Lingua* still grows at the loch, but recent search for the fungus has failed to discover it. Sydow (Monograph, i, p. 703) at one time suggested that it might belong to *Puccinia Calamagrostidis* on *Calamagrostis neglecta*, but now considers it questionable. There is no record of *C. neglecta* from Duddingston.

Excluded Species.

Uromyces Parnassiae DC. (Trail, No. 9).

This species does not exist. The aecidium on *Parnassia palustris* which was assigned to it is now known to belong to *Puccinia uliginosa* (No. 126).

Uromyces Alliorum DC. (Trail, p. 306) appears to be a spore form of *Puccinia Porri* (No. 117).

Uromyces sp. on *Triglochin maritimum*, Orkney.

This was collected, and described with drawings, by G. K. Sutherland, who discussed the species with the late Professor Trail. The manuscript and drawings are kept at the Botanical Department at Aberdeen University, but there is no specimen in the Herbarium. There appears to be no other record of *Uromyces* sp. on *Triglochin*.

Puccinia clandestina Carm. on *Scabiosa Sucissa* (Trail, No. 57).

No *Puccinia* on *Scabiosa* is known.

Puccinia Senecionis Lib. (Trail, No. 84).

This has not been found in Britain. *P. Senecionis* Cooke is a synonym for *P. expansa* Link (No. 34).

Melampsora Ribesii-purpurea Kleb.

The records given by Trail under *M. mixta* Schl. (Trail, No. 115) may refer to this species, but the only specimens of *Melampsora* on *Salix purpurea* in the Herb. Trail. belong to *M. Larici-epitea* (No. 188).

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The Work of Laurence Baxter Stewart.

By R. J. D. Graham.

Stewart joined the staff of the Royal Botanic Garden, Edinburgh, in 1895, and, except for a brief period in 1901 and the time of his war service, his life was given to the Garden. It was his brilliant work on vegetative propagation by means of cuttings which attracted most attention both in the horticultural and the scientific world. This success was achieved through careful observation and ingenious experiment, in which he never admitted defeat. His was essentially a "green thumb," and plants grew for him.

Propagation by cuttings means the isolation from their previous food and water supply of plant portions not specially adapted for independent existence. The art of the propagator is to bring out of the severed plant portion the potentialities of wound protection and organ restitution which it possesses. It is the creed of Edinburgh (1) that all plants can be propagated vegetatively by cuttings. Stewart not only believed this, but his energy was devoted to the most expeditious method of obtaining the desired result (2). In no case was a method deemed a success which did not deliver 90 per cent. of rooted cuttings (3). The results achieved may for convenience be considered under four headings: (1) Selection of plant portion for the cutting; (2) preparation and insertion of the cutting; (3) creation of a suitable environment for the cutting; (4) special features displayed by cuttings.

Plants normally offer no difficulty in the selection of the portion for cuttings. A short terminal portion of stem with at least two buds is severed and utilised as a cutting. Plants such as Ash, Sterculia, Opuntia, large-leaved Rhododendrons offer a problem by the large pith area present in their main axis. Branches, however, have a very much reduced pith, especially at their point of origin from the parent axis. Pollarding or pinching the main axis encourages these side growths, and thus the problem is surmounted. In Opuntia the pith is reduced at the base of each segment, and here the cutting is taken.

Most Monocotyledons differ from Dicotyledons in that the actual cutting forms no permanent portion in the new plant, but only serves as "a sucking bottle" for the regenerative growths which arise from its lateral buds. It is therefore necessary when selecting cuttings of Asparagus and Smilax to take pieces low down in the scale leaf region where the buds have not developed. Philesia also forms buds at the base of the cutting, and it can easily be propagated if small cuttings are selected. Two buds generally develop, and when the parent cutting disappears two plants are obtained from one cutting. Dracaena and Witsenia are among exceptional Monocotyledons, in that, if cuttings be planted upright, the terminal bud continues to grow and forms an extension of the severed shoot. Cutting back the leading shoot of Restio and Bamboo forces lateral buds into growth, and the vigour of the plant passes to the side shoots, which form the best cuttings. Lilies, which do not form bulbils naturally, will produce these if the flowering shoot is placed horizontally in a frame. These bulbils give a year's start to the plants raised in this way over seedlings.

The position of the severing cut may prove a factor in determining expeditious results. The cut is commonly made at the node, but in Clematis rooting in fourteen days is observed if the severance be made through an internode. Schizophragma proved hard to root in Edinburgh until it was discovered that the branches borne on the climbing wood rooted easily. On the other hand, pieces of ivy which have produced climbing roots develop ordinary roots slowly when used as cuttings.

The time at which cuttings should be taken can only be determined by experiment. A general guide is to take the cuttings when the season's growth is completed. The end of the season's growth does not refer to any climatic division of the year, but is peculiar to each plant and each season. For Azaleas it is the last fortnight in June, and for Beech, when the last two leaves on the twig develop, in August. At the end of the season's growth food reserves sufficient to carry on the cutting are present, and at the same time cells capable of wound protection and organ reconstruction are abundant. Stewart had cuttings taken from plants every month. From the data obtained charts were prepared showing the precise

season at which the best and most speedy results were obtained. A monthly calendar has been made out from these charts and is printed as an appendix. The data apply specially to Edinburgh, as the season's growth varies with the locality.

The preparation and insertion of the cutting was given great consideration by Stewart. A clean cut is a prerequisite for rapid healing, and a transverse cut gives the minimum area to heal. "When the wood is stiff make a sloping cut and then pare transverse; if brittle, notch the cut to avoid fracturing the end." The treatment of plants with large piths has already been mentioned. Resin or latex which flows out over the cut surfaces hinders propagation. Normally removal of the hardened resin after the end of the cutting has been exposed to air suffices, but where the resin is copious, plunging the cut end into nearly boiling water is efficacious. Cuttings with latex should be inserted in dry sand after the bleeding has stopped. In the propagation of certain decorative and economic plants the presence of anthocyanin and associated substances delays rooting. *Laurus nova zelanica* with its dark stem, and Camphor (4), when the oil content is high, will root expeditiously if the selected wood is subjected to preparatory blanching on the tree. It was also found that *Pyracantha angustifolia* will root more easily if the spines be removed.

The retention of the lower leaves on cuttings was advocated by Stewart for the following reasons. There was less healing to be accomplished, time is wasted in their removal because "the cutting itself sheds them if too many," and the lower leaves are important in decorative plants. The use of a "dibber" or pointed instrument for inserting cuttings was condemned because of the danger of an air pocket between the base of the cutting and the rooting medium. The rule is to hold the cutting between forefinger and thumb and press gently into the medium "just deep enough to make the cutting stand erect." No pressure was used to level the medium after insertion, as "watering levels the surface and does all the firming necessary." When cuttings are planted in open ground the insertion must be deep enough to avoid throwing out by frost.

The future welfare of the cutting depends on the creation

of a suitable environment. The factors of the environment most easily controlled are the rooting medium, water supply with which aeration is associated, temperature, and disease.

Sand was Stewart's favourite rooting medium in unheated frames, because "air can pass freely through it, and this is one of the essentials in propagation." The use of sand implies the immediate removal of rooted cuttings, as "the sand contains little food material, and if the cuttings are not potted immediately they soon die." The substitution of quartz sand for river sand containing silt reduced the rooting period by one-third. Ground pumice stone, if available locally, is a fair substitute for quartz sand. When plants were to remain in the propagating frames until planting out, a little humus—loam, leaf soil, or peat—according to the class of plant, was incorporated in the rooting medium. Stewart's commercial spirit did not normally encourage this leisurely use of expensive equipment. In heated cases coconut fibre was the rooting medium, as sand became waterlogged in heat. Where only a few cuttings are to be grown, the best results are obtained from filling a 4-inch pot with sand and placing the cuttings round the side of the pot. In warm weather the pot may be stood in a saucer of water and, if necessary, covered with a bell glass. Overhead watering is sufficient in cool weather.

The possibility of controlling or altering the acidity of the rooting medium was explored from 1920 onwards. Small (5) quotes Stewart as saying: "If Small be right we should make the ends of cuttings acid when we want roots." Stewart's method was to water the frames with 2–3 teaspoonfuls of vinegar to a gallon of water. Further researches were carried out by Dr. E. I. Noble (6) and Dr. Edith P. Smith (7).

The significant point in water control is that the cutting must never wilt. This is secured in unheated frames by frequent (hourly) syringing with water of the same temperature as the frame, but in frames with bottom heat the ascending water-vapour automatically controls watering. In extreme cases the frames which were given a northern exposure were shaded with tiffany to prevent wilting. Apple cuttings, which are very liable to water loss, were successfully rooted by severing the cutting under water. With vigorous cuttings in certain plants slight drying before insertion favours callus

formation and rooting. Xerophytic plants root best in sand in an open house, water being applied as necessary.

Temperature control is an equally important factor. Thermostats, electric or hot water according to the source of heating, are invaluable, and as a further precaution against fluctuations in temperature the frames are housed inside a glass house (8). The sun frame—borrowed from the French—is an ordinary sand frame jacketed inside another frame and exposed to the full sunshine, and watered half-hourly. *Erinacea pungens* and Double Gorse were rapidly rooted, success depending on bright sunshine. If cloudy weather supervene after the frame is set up no success is looked for. This suggested that the sun's rays have some effect other than a source of heat, and experiments were carried out using Vita glass (9). The cost of the installation of such frames exceeded any benefit recorded.

The health of all cuttings was maintained by scrupulous cleanliness, no dead leaves or cuttings being allowed to remain in the frames. The remedy for grey mould was watering with a pink solution of potassium permanganate, and this, Stewart maintained, not only checked disease but accelerated rooting.

The first thing a cutting does, according to Stewart, on being placed in a propagating frame is to "seal the cut end by decomposition of the cells which have been cut through." Thereafter in the majority of cases callus formation commences usually from the cambium, but in the Bignoniaceae the medullary rays and pith are also active in callus production as well. The callus when massive shows curving zones of growth, and the direction of growth can be determined by suitable stimulation. Massive callus development was likened by Stewart to a malignant growth which absorbed water and would keep the cutting in life but delayed the production of roots. Paring of the callus is recommended in such cases, thus allowing the parent cutting to reassert control, when rooting almost immediately takes place. This was well illustrated in members of the Proteaceae, the roots when developing growing at right angles to the stem, and thus demanding potting at the earliest possible moment to avoid damage to the roots. In contrast to this lavish production of callus other plants produce little or no callus. These are

either plants in which rooting takes place with great rapidity, *e.g.* Coleus in twenty-four hours, or those in which the march of events is slow, for example the Australian Leguminosae. In the second case, small cuttings with their reduced water demand frequently give success.

Cuttings which had rooted when removed from the frames were placed in a box of damp Sphagnum and then potted into "thumbs" without washing the roots. The plants in their pots were immediately replaced in their frame until established. There was thus no check caused either by drying of the roots or violent fluctuation of temperature.

Not infrequently plants can be raised from portions which do not have buds on them, such as internodal cuttings, root and leaf cuttings. Commonly a cutting includes at least one bud. Such selection is unnecessary in *Acanthus*. Any internode, portion of root or leaf may be used as a cutting, and a point which always interested Stewart was the juvenile characters of the young plants so raised (10). Root cuttings give more expeditious results in Spathodea, Ailanthus, Calycanthus, Cladrastis, Aralia, and Prunus; also in Crambe, *Anchusa italica*, *Primula*, *Drosera binata*. In Pelargonium and Bouvardia plants raised from root cuttings often varied from the parental types, a matter investigated at the John Innes Institute (11) on material raised by Stewart.

Leaf cuttings from foliage leaves are utilised in Begonia, Melastomaceae, Gesneraceae, Acanthaceae, and Crassulaceae. If only one plant is required the leaf is inserted whole, whereas if more plants are needed the main veins are cut. A new plant will develop from the distal end of each cut, and the more the cuts the more juvenile the character of the plants. In many cases of leaf cuttings roots are produced easily but shoot development is slow. To secure success the leaves must be inserted early so as to ensure shoot formation before the end of the season, otherwise the leaf dies. Brownea is an exception, in that the large basal leaf callus can be kept growing for 3–4 years, and the leaf finally disappears before a shoot develops. The leaflets of Zamioculcas are interesting in that first a tuber is formed, then roots, and then a shoot develops from the upper side of the tuber. *Acanthus* is so versatile that the petiole will produce a plant, a result which can also be attained with difficulty in Begonia.

Storage scale leaves are commercially used for the multiplication of Monocotyledons. The difference between propagating from a storage leaf and a foliage leaf is that the foliage leaf roots first while the storage leaf forms a bud first.

Where plants exhibit horizontal branching with marked dorsiventrality, as in many Conifers, Gardenia, Napoleona, branch cuttings develop into dorsiventral plants to which varietal names of *nana* or *pendula* are given. Sooner or later these plants develop a leader from a plastic bud. This also happens in certain cases when the leader is removed from a tree. The dormant plastic buds grow out as upright radial shoots, which can then be utilised for propagating symmetrical trees. A point to note is that the branch cutting of Gardenia flowers every year in its dwarf form, while seedling plants take years to reach the flowering stage (12).

Plants with highly developed hypocotyl, such as Bursera, many of the Proteaceae, and some Sterculias, lose these structures when raised as cuttings. This is an advantage, since cultivating these plants from seed demands special care not to bury the hypocotyl, or the plants die. Anatomically a hypocotyl is regenerated, as was shown by M'Martin (13).

It has long been accepted that inverted cuttings of such plants as Laburnum, Beech, Hazel, Willow, and Vines never increased in thickness. An inverted cutting of *Salix alba*, in which the inverted portion was 36 inches long, proved after ten years that thickening in the inverted portion did take place, but was initially less than in the leader growing normally (14).

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Propagation Calendar.

Plants arranged alphabetically under the month in which insertion of cuttings yield good results; equal results—90 per cent. or more rooted cuttings—obtained by inserting cuttings in months shown by Arabic numerals.

The Roman numeral indicates the month in which rooted cuttings are obtained.

January.

Berchemia racemosa, V.
Buddleia globosa, IV.
Buxus balearica, VII, 1–12.
Forsythia intermedia Vitellina, 1–12, see June.
Kalmia latifolia, VI, 11.
Lycium chinense, 1–12 less 9, see July.
Maddenia Wilsoni, 1–3 (2 months).
Meliosma cuneifolia, 1–4, see March.
Platyosprion platycarpum, V.
Prunus spinosa purpurea, V.
Sycopsis sinensis, 1–4, 7, 11, 12 (3 months).
Vaccinium padifolium, III, 1–8.

February.

Gaultheria procumbens, VI.
Helianthemum alyssoides, 2–5 (1 month).
Helianthemum hirtum, 3, 6, see June.
Illicium floridanum, V.
Pieris formosa, IV.
Tamarix Pallasii, 2–8 less 5, 6, see July.

March.

Acanthopanax spinosum, 5, 7, see July.
Calycanthus occidentalis, 7, see July.
Carmichaelia flagelliformis, 3–9 less 6, see August.
Caryopteris Mastacanthus, VI, 4.
Choisya ternata, 3–9, see August.
Cistus florentinus, V, 4.
Cistus purpureus, V, 3–5.
Clethra alnifolia, 3–8 less 6, see August.
Colutea longialata, 3–9 less 5, 6, see July.
Discaria serratifolia, 3–10 less 6, 7, see April.
Elaeagnus pungens, 3–5, see May.
Eleutherococcus sp., 3–6, see June.
Eucommia ulmoides, VIII.
Fontanesia Fortunei, 3–8, see July.
Griselinia littoralis, 3–9, see May.
Hydrangea paniculata, 3–9; *grandiflora*, see June.
Hymenanthera crassifolia, 3–9, see May.
Kalmia angustifolia, V, 3–5.
Laburnum alpinum, VI.
Laurus nobilis, 3–9, see May.
Lavandula vera, V, 4, 8, 9, 12.
Ledum latifolium, 6–8, see August.
Leiophyllum buxifolium, VI.
Meliosma cuneifolia, VI.
Morus nigra, 3–5, see May.
Olearia nummularia, 3–6 less 5, see June.
Pittosporum tenuifolium, 4, 5, 8, 9, 11, see August.
Platanus acerifolia, V.
Populus nigra pyramidalis, IV.
Pterocarya caucasica, VI, 4.
Schizandra sphenanthera, VI.
Shepherdia canadensis, 4, see April.
Stachyurus chinensis, VII.
Viburnum Opulus, 3–9, see June.

April.

Andromeda japonica variegata, 4–9, see July.
Bruckenthalia speculifolia, VII.
Calluna vulgaris, 4–11, see July.

Calycanthus occidentalis, VI.
Catalpa hybrida japonica, VII.
Celastrus scandens, 4–9 less 6, see May.
Cladrastis tinctoria, 6, see June.
Clerodendron trichotomum, VII.
Clethra canescens, VIII, 6.
Corokia Cotoneaster, 4–9 less 5, 6, VII.
Cotoneaster Simonsii, VII, 9.
Discaria serratifolia, VII.
Hippophae rhamnoides, VII.
Jamesia americana, VII, 10–4.
Myricaria germanica, VII.
Neillia opulifolia var. *lutea*, 5, 7–9, see July.
Purshia tridentata, VIII.
Santolina viridis, VII.
Shepherdia canadensis, VII.
Skimmia japonica, 4–8, see July.
Smilax aspera, VII.

May.

Abelia spathulata, VI, 6.
Amorpha fructicosa, VII.
Aucuba japonica, 5–8, see July.
Celastrus scandens, VII.
Cornus alba, VII.
Deutzia discolor fasciculata, 8, 9, see August.
Elaeagnus pungens, VIII.
Enkianthus pallidiflorus, VII.
Enkianthus pendulus, VII.
Enkianthus recurvus, VII.
Garrya elliptica, ♀, XI, 9.
Griselinia littoralis, VIII.
Helwingia rusciflora, 5–9 less 6, see July.
Hymenanthera crassifolia, VII.
Jasminum humile, 5–7, see July.
Laurus nobilis, VII.
Leucothoe Catesbaei, VII, 5–7.
Microglossa albescens, 5–8, see July.
Morus nigra, VII.
Phlomis fruticosa, 5–8, see July.
Phillyraea decora, 9, see September.
Prunus cerasifera atropurpurea, VI.
Stephanandra flexuosa, 5–9 (1 month).
Syringa persica, VII, 7.

June.

Arctostaphylos alpina, VII.
Atriplex canescens, VIII.
Caragana arborescens, 6–9, see August.
Ceanothus azureus (Gloire de Versailles), 6–8, see July.
Cladrastis tinctoria, VII.
Coriaria myrtifolia, VIII, 6–9.
Cornus stolonifera, VII.
Eleutherococcus sp., VII.
Enkianthus latiflorus, X.
Enkianthus Palibinii, X.
Enkianthus tectus, VIII, 7.
Euonymus verrucosus, IX.
Fabiana imbricata, 6–9 (1 month).
Ficus Carica, VII, 7.
Forsythia intermedia Vitellina, VII.
Helianthemum hirtum, VII.
Hydrangea paniculata grandiflora, VII.
Leucothoe racemosa, VIII.
Olearia nummularia, IX.
Parrotia persica, VII (13 months).
Pernettya mucronata, 9, see September.
Rhodotypos kerrioides, 7 (2 months).
Stephanandra Tanakae, VII, 6–8.
Viburnum Opulus, VIII.

July.

Acanthopanax spinosum, VIII.
Andromeda japonica variegata, VIII.
Aristolochia heterophylla, VIII.
Aucuba japonica, VIII.
Baccharis patagonica, VIII, 11, 12.
Calluna vulgaris, VIII.
Calycanthus occidentalis, VIII.
Cassandra calyculata, VIII.
Ceanothus azureus (Gloire de Versailles), X.
Clematis grata, VIII.
Clematis Jouiniana, VIII.
Colutea longialata, VIII.
Coronilla emeroides, VIII, 8, 9.
Corylopsis spicata, VIII, 8.
Cydonia japonica, XII.
Cytisus praecox, X.
Desfontainea spinosa, X, 7–9.
Diervilla florida, VIII, 7–2 less 9, 10.
Escallonia rubra, VIII.
Fontanesia Fortunei, VIII.
Hedysarum multijugum, VIII.
Helwingia rusciflora, VIII.
Indigofera Gerardiana, VIII, 8.
Jasminum humile, X.
Kerria japonica, VIII, 7–9.
Lindera Benzoin, XII, 9.

Lonicera bella rosea, VIII, 7–11.
Lycium chinense, VIII.
Lyonia ligustrina, X, 7–9.
Microglossa albescens, VIII.
Neillia opulifolia var. *lutea*, VIII.
Nuttalia cerasiformis, ♀ ♂, VIII.
Osmanthus Aquifolium ilicifolius, 8, see August.
Philadelphus incanus, 7–10, see August.
Phlomis fructicosa, VIII.
Potentilla fructicosa tomentosa, VIII.
Prunus Laurocerasus schipkaensis, 7–9, see August.
Ptelea Baldwinii, VIII, 7–9.
Pyrus arbutifolia, VIII, 7–9.
Ruta graveolens, VIII, 8.
Skimmia japonica, VIII.
Spartium junceum, VIII, 8.
Symphoricarpus Heyeri, 7–12 (1 month).
Tamarix Pallasii, VIII.
Ulex europaeus, VIII, 8.
Wistaria frutescens magnifica, VIII.

AUGUST.

Abelia umbellata, X.
Akebia quinata, 9, X.
Arctostaphylos Uva-ursi, X, 12, 1, 2.
Aristotelia Colensoi, X.
Berberis Aquifolium, X, 9.
Caragana arborescens, IX.
Carmichaelia flagelliformis, IX.
Choisya ternata, IX.
Colletia cruciata, IX.
Clethra alnifolia, IX.
Deutzia discolor fasciculata, XII.
Ercilla volubilis, X.
Fontanesia Fortunei, X.
Hypericum hircinum, X, 8–10.
Koelreuteria paniculata, X.
Ligustrum Prattii, 9, 12, see December.
Ledum latifolium, X.
Neviusia alabamensis, X, 8–11.
Philadelphus incanus, X.
Pittosporum tenuifolium, X.
Prunus Laurocerasus schipkaensis, X.
Osmanthus Aquifolium ilicifolius, XII.
Zanthorrhiza apiifolia, X.

SEPTEMBER.

Aristotelia racemosa, XI.
Azara microphylla, V.
Bupleurum fruticosum, V.
Cassinia fulvida, XII, 10.
Daboecia polifolia, V, 10.
Garrya elliptica, ♂, V.
Lonicera etrusca, X.
Maytenus Boaria, V, 9–12.
Paliurus australis, 10, see October.
Pernettya mucronata, V.
Phillyraea decora, XI (14 months).
Senecio laxifolius, XII, 10, 11, 2, 3.

OCTOBER.

Berberis vulgaris, 11, VII.
Jamesia americana, 10–4, see April.
Paliuris australis, IV.
Daboecia polifolia, IV.

DECEMBER.

Ligustrum Prattii, VIII.

The Scottish Alpine Botanical Club Excursion, 1933.

By Robert Moyes Adam, F.L.S. (With Pls. XI–XIII.)

(Read 18th October 1934.)

The visit to Corrour was the result of an invitation from Sir John Stirling-Maxwell, K.T., to the Club to make his lodge in the Inverness-shire highlands the headquarters of their annual excursion and meeting, for a botanical exploration of the hill country of his extensive deer forest. The visit promised a unique opportunity to see and explore the fringes of Brae Lochaber and adjoining ungetatable country, so an enthusiastic Club requested the President to accept the invitation on their behalf, and to render their thanks in full measure to Sir John and Lady Stirling-Maxwell for the kindness in placing such an alluring prospect before them.

The lands of Corrour are situated in the south-eastern corner of Inverness-shire and are adjacent to the north-western district of Perthshire, while the principal streams drain towards the north and feed the higher reaches of the River Spean after it leaves Loch Laggan. This tract in highland Scotland is most inaccessible and is almost unique in this respect, for there are no roads that either cross or lead into this vast territory. Before the construction of the West Highland Railway through Corrour, which was opened for traffic in 1896, access and transport must have been a problem of considerable difficulty. The nearest track to Corrour from a highway in early days commenced in Glen Spean, near Roy Bridge. It was an old drove road, and as such is still sometimes used when herds are being driven to southern markets. From the Roy Bridge end the old road strikes south towards the big Nevis range of hills to enter a deep glen which on the southern side is known as the Leacan Pass. The track emerges at Loch Treig head, and then rises to Loch Ossian, at which point a connection links it up with Corrour. From Loch Ossian the old track commences an ascent on the south shore, and after pursuing a route for a

distance of twelve miles over rough bog and moor, ultimately reaches the Rannoch valley and the present improved and modern roadway of that glen. Such, then, are the old approaches to Corrour, which to-day can only be tackled by the sturdiest pedestrian, but are quite useless for any vehicle.

With the advent of the railway, communication with the outer world has been simplified. A station named Corrour has been built, and while it is but a mere halt perched on the elevated tract of Rannoch Moor, some 1200 feet up, it provides an easy gateway to the wild bounds of Corrour. From the station a privately constructed roadway five miles in length leads to the present lodge. A few years ago this means of approach ceased at the west end of Loch Ossian, and the intending traveller to Corrour had to resort to water transport to complete the last stage of his journey. The present lodge, which is built of stone hewn from the hillside nearby, occupies a fine commanding site a few feet above the loch level at the eastern extremity of Loch Ossian. The setting is truly grand, and the view obtained, which was enjoyed by the Club, includes a wide panorama of mountain and loch. Later, the same scene, when the waters of the loch were lashed into fury by rain and wind, and the sun shone fitfully from an angry sky, became unforgettable.

The Club party arrived at Corrour Station on the afternoon of 18th July where interest was speedily kindled by the sight of a group of Mountain Pines adorning a corner of this odd place. Eastward, in the distance the waters of Loch Ossian could be observed surrounded on all sides by many acres of thriving plantation. These added a warmth to the scene and presented evidence that some afforestation enterprise was in progress. The intervening landscape, however, looked dreary and served to show a typical patch of the fringe of the great Moor of Rannoch.

Some of this ground was examined in the hope that the rare alpine rush *Scheuchzeria palustris* might be found, but no new station was discovered, although later, beside Rannoch Railway Station, some plants were observed in splendid fruit. Identification of this rush is difficult in the natural habitat, and unless the plant is in flower or fruit it easily escapes notice.

The journey from the station to the lodge was accomplished

by car, and interest in the environs mounted higher as the shores of Loch Ossian were skirted and the first glimpses obtained at close quarters of the splendid specimens of young and growing timber that fringed the shores. These impressions were, however, abruptly terminated by the speedy arrival at the white gate of Corrour. Here Sir John, in kindly anticipation of our coming, was at hand, and took the Club party under his wing. Soon thereafter, in company with Cameron his chief forester, a route was being pursued into the heart of the young plantations, and for the rest of the day, under their joint and expert guidance, a fascinating time was spent.

The Club was to see much of the forest side of Corrour during their stay, but even in this short preliminary contact with it enough was witnessed to demonstrate how absorbed is Sir John in the subject of Forestry. Experimental plots and trial grounds lay on all sides, signs of the devotion, time, and skill that have been expended throughout a lifetime to wrest from an unwilling soil secrets that might help to solve the problems confronting those who contemplate profitable afforestation over the Highland areas. The forest enterprise at Corrour dates back about forty years. At that time natural timber of any kind was practically non-existent except for a scraggy natural birch wood on Leiter Dubh, a knoll above Loch Ossian. Even the common Rowan was a very rare tree, a surprising fact in view of its frequency in most Highland areas.

Planting at Corrour was begun in the year 1893, and little was observed from these early experiments to encourage the grower. Scots Pine was selected at this early date to be the principal timber tree, but both this and other trees which were tried failed dismally to give promise of a forest success. A remnant still remains of these trees to bear out the melancholy record of failure. But while these early misfortunes were endured, experience was gained, and about the year 1903 an intensive study of the subject was begun which has been continued up to the present time. Many of the methods employed and used in 1893 were revised. New ways and systems to establish healthy forest were adopted and put into use. Experimental planting continues, and now a vast acreage of young forest testifies to the determined effort to

Corrour. A view in the Deer Forest, showing Strath Ossian and the site of the Lodge beside Loch Ossian. Some of the young forest planted on the hillside appears in the foreground.

Robert Moyes Adam.

surmount the problem of growing trees on an elevated moorland of the Highland type. To-day planting has been carried to an elevation of 1680 feet.

A brief summary of certain procedure in this afforestation work at Corrour may be of interest. The planted and plantable ground is divided into compartments and a careful record kept of treatment each has received. Basic slag, sometimes mixed with sand, for example, has been applied as a top-dressing in certain areas with beneficial results. Hot and ground lime have also been used in a similar way. A map based upon this subdivision of the land and arrangement has been printed and is available for others to gain an accurate estimate of the work done.

The trees experimented with include most of the better known timber trees, but beside them are to be noticed quite a few of the newest introductions from Eastern Asia and China. It was instructive to learn that the Scots Pine was regarded as quite unsuitable for general planting, especially in view of the many excellent specimens that grow to maturity in a wild state and at a similar elevation in the Rannoch valley, 20 miles to the south. No wild Scots Pine are alive to-day at Corrour, but old skeleton stems are commonly seen in the peat. Another surprising fact was revealed in the rarity of both Alder and Rowan, perhaps two of the commonest trees in the Highland area. These prove obstinate and difficult to cultivate here. Other broad-leaved trees like Acer and Beech can succeed in cultivation if given a modicum of shelter and ample protection from rodents and deer.

Of the timber trees that now give promise of success, outstanding are the Norway Spruce and Sitka Spruce. Indeed, it would appear that both climate and soil at Corrour are pre-eminently suited to these species. Larch as a timber tree disappoints except where gravel and good drainage are obtainable.

Peat soils dominate the ground, and they vary in depth from a few inches to several feet. Glacial drift overlays the basic rocks over most of the area—sometimes as a tenacious clay, occasionally with quantities of boulders. Two basic rocks enter into the geological character, the one a granulitic type and the other a hard schist. Where the former is overlaid soil is at its poorest. To combat this difficulty of intract-

able peat a modified application of a Belgian forest-planting method has been adopted with much success. It involves the creation of special nurseries where prospective forest trees are grown after the seedling stages are passed. Over the ground selected for the planting large blocks of turf measuring 2 feet each way are dug out. These are arranged in the reverse position in rows on the strips of untouched peat, and left to weather during a winter season. The following spring young seedling trees are taken from the nursery and inserted or planted into these weathered turf blocks (see Pl. XIII). These seedling trees are then left to grow and develop without further interference. After a lapse of two years or so the young trees will have quite recovered from any check and have developed good root systems. At this final nursery stage the plants are in a condition for transplantation to permanent quarters. This involves the carriage of the turf containing the young established tree to the spot where it is intended to form forest. The turf and tree as a unit is simply laid in position on the surface of the moor on the top of any existing vegetation and then left to its fate. The method seemed rough and crude, but the success, as observed at Corrour, left no doubt as to the general health and vigour of the young specimen trees thus treated. None of them, of course, was of great age, but the party were informed that plants so treated can resist well the evils of drought, and in the presence of excessive moisture can secure for themselves ample drainage. The rainfall at Corrour measures about 70 inches per annum. Nurseries, it was noticed, were formed either on or beside areas selected for planting by this method.

But the intriguing forest had to be subordinated to the claims of the hills, and it was during the evening of the first day that stock was taken of the array of summits that comprise Corrour, and a decision reached as to the hill likely to yield the most productive day. Thus it happened that Beinn Eibhinn (3611 feet) was singled out as the initial mountain project. In the descriptive language of the Gael this name signifies "The beautiful hill," and therefore not unworthy to be chosen as the first to be investigated of the seven tops of Corrour that rise above the 3000-foot contour. The route followed led up a slope north-east of the lodge,

Beinn Eibhinn. A view of the Northern Slopes, with the Creag Meaghaidh Range in the distance.

ROBERT MOYES ADAM.

after crossing the bridge that spans the Uisge Labhair. After an ascent to 1800 feet the party arrived at a small hill cairn which is a fine view-point on the ridge above Strath Ossian. The slope to this strath is steep and is cut by several defiles and ravines, the slopes of which yielded some rich fern ground. The exploration was carried through by one member who found the high-level journey too strenuous. Plant life encountered on the Eibhinn ascent was typical of rich moorland pasture, with places that were characteristic of a wind-swept zone, both the *Calluna* and *Vaccinium* exhibiting compact and cushion form. From this subsidiary cairn and while trekking over a wettish area at an elevation of 2000 feet, fine plants of *Betula nana* were observed growing on the firmer peat hags along with *Vaccinium* and *Eriophorum*. During the progress of the party heavy clouds continued to hug the highest parts of the mountain, and in view of this condition a traverse to the north and towards the western flank was made. This north-west side showed considerable scree, with occasional damp corners; but plant life became scarcer, and above the 2800-foot contour arid conditions reigned over the major portion of the slope. Towards the summit the whole mountain-top presented a vast heap of detritus with scarcely a trace of a moss. Not a vestige of snow was visible, although here and there in hollows signs of recently melted drifts were in evidence. Beinn Eibhinn has two considerable corries towards the north, and from the summit a very steep declivity descends to their base. A minor top called Mullach Coire nam Nead, which is the western spur of the main peak, has a fine buttress and some damp recesses, and these were examined. Conspicuous among the plants of the buttress were the Roseroots and Kidney-leaved Sorrel. The ascent of a gully beside the buttress brought the party to the long dry ridge of Eibhinn, but the threat of a rainstorm delayed progress. The clouds, however, lifted and the summit was gained, but poor visibility prevented the fine mountain panorama to the north-west and north from being seen to advantage. The summit is singularly well placed for a view of the Laggan valley and the Creag Meaghaidh range.

From Eibhinn a slight descent of some hundred or two feet and a slow rise towards the north-east and the summit of Aonach Beag was topped. This mountain is out of the exact

bounds of Corrour, but by including this hill a circular tour and descent was made interesting and easy. This climb brought its special reward by the discovery of numerous plants of *Cherleria sedoides* growing quite happily among the stony debris of the top at 3646 feet. In the course of the day one plant, curiously it seemed, had so far eluded the hunter, this was *Silene acaulis*. The descent from Aonach Beag was attended by no special finds, but the exceptional dryness of the rocks and slope made this part of the journey tiresome. Once into the great amphitheatre of the northern corrie and below the summit some plants like the Cornel and Vaccinium relieved the monotony of a series of peat hags, while the great slopes of Eibhinn, which had been traversed earlier in the day, seemed to tower aloft in formidable array. In the corrie of Mullach Coire nam Nead the two tiny lochans that nestle at its base were visited, but nothing outstanding was noticed. Loch Gulbin, which for a great part of the day had been visible to the west, was ultimately reached, and its lonely aspect was considerably intensified by a sharp thunderstorm that passed overhead. From the shores of Loch Gulbin the path was struck that ultimately led into Strath Ossian. On the side of the path in Strath Ossian an unexpected find was made—a fine specimen of *Pernettya nigra* in full flower growing among old stones and gravel. The plant was obviously self-sown. Later it was ascertained that the species was in cultivation at Corrour—a few miles distant. The find was none the less interesting and remarkable considering the situation, and, further, provided a splendid example of a New Zealand shrub apparently quite adapted to colonise a part of the wilderness of Corrour, about 1400 feet above the sea.

On the return to the lodge the party were pleasantly surprised by the presence of that veteran Sir Herbert Maxwell, Bt.

The second mountain excursion was planned to examine Chno Dearg (3433 feet), and for this venture the party set forth under stormy conditions of rain and wind. The hill presents an inviting prospect because of the steep face that is thrown down to Allt Feith a Ealaidh. After leaving the lodge a path was followed through plantations to the north of Loch Ossian. The slope presented a gentle gradient for part of the way, then after the first 500 feet had been ascended

Scheuchzeria palustris. Group of wild plants in fruit, wet bog, Moor of Rannoch, Perthshire.

Forest Nursery. The Belgian method. Showing young trees planted and growing in peat blocks. In front, specimens after removal from nursery to permanent quarters.

Robert Moyes Adam.

rougher ground was reached with frequent peat hags. Then followed a vast hollow in the midst of which lay Lochan a Lap. Very barren moorland with much Cloudberry and Bilberry dominated this territory. The waters of the lochan are shallow, with aquatic plant life of a Highland type. An island in the loch was found to be plentifully carpeted with fruiting Cloudberries, sufficient being collected by one member of the party to fill a dish for the dinner-table. Very old peat and tough heather marked the route after Lochan a Lap, and when the last part of the descent was in progress towards the Allt Feith a Ealaidh the rainstorm became so violent that shelter was taken under one of the many huge boulders that are strewn about the hill-side. After this interruption the party were thoroughly saturated with water, but undeterred from making the ascent towards the big corrie of Chno Dearg. For the task the weather was very bad and shelter was frequently sought under the lee of the crag while violent rainstorms swept the hillside. After awhile a lull in the storm encouraged the mists to lift, but never high enough to expose the summit. They rolled round it in a threatening manner and continued to do so during the remainder of the time the Club were on the hill. The crag of Chno Dearg is formidable and impressive, but, except in wet weather, is likely to be dry and lacking in favourable conditions for vegetation. About the centre a rent in the cliff displayed a miniature cascade, and by the sides and the ledges near where the water fell quite a rich little corner was explored. But in general the coire had a dearth of plant life. While the clouds showed signs of shifting higher, the wetness of the party hastened the decision to end further exploration and a descent in a diagonal direction was made. *Silene acaulis* was again a notable absentee from the plants observed, a surprising fact which tended to confirm the paucity of the flora of the hill-tract explored. Meanwhile the dense mists prevented the investigation of the presence of *Arctostaphylos alpina* which Sir John had reported growing abundantly on the summit of Chno Dearg. At Inbhircala the track from Loch Gulbin was joined, and a walk through Strath Ossian in pitiless rain hastened the return to dry clothes at the lodge.

On the morning of the 21st the good weather returned, but after the buffetings of the two previous days, a modest

programme was carried through. It was the mountain group to the south of the lodge that claimed attention and of which Carn Dearg (3084 feet) is chief. Sometimes known as the hill of the three cairns, it presents the smoothest of outlines and a featureless summit. The ascent was again made through the forest zone at the base. The party again enjoyed the guidance of Sir John, who remained out with them all day. After a steady pull up the easy gradient the wide and extensive summit plateau was reached. Towards the highest levels a few flushes came in for scrutiny, but disappointing numbers of alpine plants were observed. On the roughest ground the party were gratified by the sight of *Silene acaulis*. A long pause at the highest cairn gave opportunity for a splendid view to be obtained, the mountain-tops in endless succession on all sides standing out with fine effect.

From the cairn of Carn Dearg a gentle slope towards the north-east led to the dip which separated Mam Bhan, a beautiful grassy hill with excellent pasture. Over the boggy area in the depression further plants of *Betula nana* added interest to the walk. From Mam Bhan another easy slope rose towards Sgor Gaibhre (3128 feet). This was noted to be a granite hill with grassy flanks, except on the north-east face, where a formidable cliff composed of great granite slabs fell quickly down to the wide stretch of moor that separated this mountain from the mighty mass of Ben Alder. The plant life showed a limited variety, and although a wide circle was covered on the hill the party had to be content with modest rewards. The return to the lodge was made by Coire Chreagaich and the principal stream that drains this glen.

The final phase of the meeting was spent admiring the collection of alpines, native and alien, in the garden of the lodge. It was an amazing collection which in the variety seen paid further tribute to those who have toiled to cultivate and make the desert blossom as the rose. Corrour garden is as unique as the situation—over 1200 feet above the sea—perhaps one of the highest gardens in the land and with more to suggest the lay-out of an Italian villa than that of a Highland shooting-lodge. The profusion of blossom on the shrubs and the abundance of flower among the herbaceous groupings was a sheer delight. Outstanding were the handsome masses

of the Himalayan *Cyananthus lobatus*. It was a group to be envied and undoubtedly thoroughly at home. All the paths are paved and suggest a pleasing causeway, while the same stone element is used to furnish and divide the beds into compartments, where everything seemed to be in splendid form. A retaining wall which supported part of the terrace below the lodge was a feature that showed off with fine effect many rock-loving species. The centre piece of the garden was a circular lily pond, which looked particularly charming from the lodge windows.

But the details of this garden were too numerous to outline. Enough was seen to convince the visitor how well suited to this unusual environment are some of the alpine plants of recent introduction. Outside the garden among the many plants pointed out were quite a host of the newer Rhododendrons.

But this feast of interest drew to a close on the morning of the 22nd, and with a farewell glance at the lodge and a brief acknowledgment of thanks to host and hostess, the party thereafter motored to Corrour and caught the morning train, thus terminating a notable event in Club history.

The following list shows the noteworthy species seen during the excursions: *Thalictrum alpinum* Linn., *Cochlearia alpina* Wats., *Viola lutea* Huds., *Silene acaulis* Linn., *Cerastium alpinum* Linn., *Arenaria sedoides* Druce, *Rubus Chamaemorus* Linn., *Saxifraga oppositifolia* Linn., *S. stellaris* Linn., *S. aizoides* Linn., *S. hypnoides* Linn., *Parnassia palustris* Linn., *Sedum roseum* Scop., *Drosera rotundifolia* Linn., *R. anglica* Huds., *Angelica sylvestris* Linn., *Cornus suecica* Linn., *Galium boreale* Linn., *G. saxatile* Linn., *Solidago Virgaurea* Linn. var. *cambrica* (Huds.), *Gnaphalium supinum* Linn., *Saussurea alpina* DC., *Hieracium alpinum* Linn., *Lobelia Dortmanna* Linn., *Vaccinium uliginosum* Linn., *Azalea procumbens* Linn., *Armeria maritima* Willd., *Veronica humifusa* Dickson, *V. alpina* Linn., *Pedicularis palustris* Linn., *Polygonum viviparum* Linn., *Oxyria digyna* Hill, *Betula nana* Linn., *Salix herbacea* Linn., *Empetrum nigrum* Linn., *Juncus biglumis* Linn., *Carex saxatilis* Linn., *Cryptogramme crispa* Br., *Cystopteris fragilis* Bernh., *Polystichum Lonchitis* Roth, *Lastrea aristata* Rendle et Britten var. *alpina* Moore, and *Lycopodium alpinum* Linn.

OBITUARY NOTICES.

Harry Frank Tagg, 1874–1933.

Harry Frank Tagg, born in Maidstone in 1874, was trained at Swanley College, Kent, and thereafter for nearly forty years occupied with distinction the post of Assistant in the Museum at the Royal Botanic Garden, Edinburgh. In this capacity, in 1904, he was granted long leave of absence for the purpose of collecting botanical material in other parts of the world, and in the course of a prolonged tour he crossed the Pacific and visited Australia and New Zealand.

In the preparation of museum exhibits Tagg was an expert, while many of the methods he adopted for the preservation of botanical specimens were unique, and the excellence of his work in this department is enduring evidence of his manipulative skill and ingenuity.

The earlier part of his career was devoted to the study of plant pathology, especially with regard to the diseases of timber, and during the War he performed valuable work as Scientific Officer to the Timber Supply Department under the Board of Trade.

In later years Tagg turned his attention to systematic botany, and became an authority on the genus *Rhododendron*. The many descriptions of new species which he published from time to time bear witness to the fact that his knowledge of this complex genus was both wide and deep, and it was only natural that he should be invited to co-operate, as he did with conspicuous success, in the preparation of that important work *The Species of Rhododendron*, published by the Rhododendron Society in 1930.

Tagg, who was a Fellow of the Linnean Society, became a member of the Botanical Society of Edinburgh in 1902, and was a frequent exhibitor at the Society's meetings. He also contributed a number of original papers to the *Transactions*.

M. Y. O.

William Grant Craib, 1882–1933.

Professor William Grant Craib was born at Banff on 10th March 1882 and died on 1st September 1933, after a few hours' illness, at Kew, where he had been spending part of his long vacation working on the Siamese flora.

Craib received his early education at Banff and Fordyce Academies, and later entered Aberdeen University, taking the degree of M.A. in 1907. In 1908 he received a temporary appointment as Acting Curator of the Herbarium at the Royal Botanic Gardens, Calcutta. While in India he made large collections of plants from the North Cachar Hills, which he subsequently named. In 1909 he accepted the post of Assistant for India at Kew. At this time large consignments of Siamese plants were being received, and these roused Craib's interest in the flora of that area. From 1911 onwards he published descriptions of numerous species under the title *Contributions to the Flora of Siam*. In 1925 he commenced the publication of what must be considered his principal work, his *Flora Siamensis Enumeratio*, and at the time of his death the first volume had been issued as well as the first part of Vol. II. The manuscript of the second part of Vol. II had also been sent to the press.

During his undergraduate days Craib had shown his interest in the plants round Banff, and in 1912 he published the *Flora of Banffshire*, a list of flowering plants and ferns with their local distribution. In 1915, on the invitation of Professor Bayley Balfour, he became Lecturer in Forest Botany and Indian Forest Trees in the University of Edinburgh, and while holding this post he published a series of papers on the *Regional Spread of Moisture in the Wood of Trees*. He was elected a Fellow of the Botanical Society in December 1915, and in 1920 was elected a Fellow of the Royal Society of Edinburgh and also of the Linnean Society.

In 1920 he was appointed to the Regius Professorship of Botany at Aberdeen. Here he entered enthusiastically into the work of teaching and research. He was a stimulating teacher and was able to inspire his students with some of his own enthusiasm. His botanical colleagues have lost a distinguished systematist who was always willing to give help and valuable advice.

M. W.

TRANSACTIONS

OF THE

BOTANICAL SOCIETY OF EDINBURGH

SESSION XCIX

Some Observations on the Decay of Timber.

By Malcolm Wilson, D.Sc.

(Read 17th January 1935.)

Although Dry Rot caused by *Merulius domesticus* is probably the most serious factor in the decay of timber in buildings in this country, there is no doubt that several other fungi may be frequently concerned. This fact is now generally recognised and cases of rot are more carefully investigated than in the past. At one time almost all outbreaks of decay were put down to *Merulius lachrymans*, but now, owing to the work of a number of investigators—especially Mez and Falck —our knowledge of the fungi which cause rot in timber has greatly increased and diagnosis has in consequence become more accurate.

A point of considerable importance and one which has aroused much discussion and investigation is the question of the origin of the fungi causing dry rot. Several of the older investigators, *e.g.* Tubeuf (1903), believed that *Merulius lachrymans* was occasionally found on standing trees and that timber could become infected while actually in the forest; such timber, when introduced into buildings, would then lead to an outbreak of decay. Largely as a result of the investigations of Falck (1907) it is now known that a number of distinct

species were included under the name *Merulius lachrymans*. One of these, now known as *Merulius domesticus*, only occurs on sawn timber and is the cause of dry rot in buildings, while another, *Merulius silvester*, does occur in the forest.

M. silvester closely resembles *M. domesticus* but may be distinguished by certain differences in its mycelium and by the structure of its fructifications. It has been found in various localities on the Continent, but there appear to be no records of its occurrence in this country. It was, however, recently discovered in a wood in East Lothian growing on a fallen branch of the Corsican pine (*Pinus Laricio*).

Several investigators, including Wehmer (1912), have pointed out that in the past, decay resulting from attack by *Coniophora cerebella* has frequently been confused with dry rot. This fungus is sometimes said to cause a condition known as wet rot since it can only exist under damp conditions, attacking wood containing a large percentage of moisture. Like *Merulius*, *Coniophora* produces characteristic strands on the surface of the infected wood, but while those of the former are grey, often large (sometimes as thick as a lead pencil) and brittle, those of *Coniophora* are generally thin and always dark brown.

Although the fructifications of the two fungi have a superficial resemblance they can be distinguished by careful examination, since those of *Merulius* are characterised by the production of shallow irregular pores in which the spores are formed, while in *Coniophora* the thinner fructification is made up of a number of rounded wart-like projections on which the spores are produced.

The decay caused by *Coniophora cerebella* under extremely damp conditions may be as serious as that produced by dry rot. An outbreak exemplifying this was recently investigated in Edinburgh. The flooring on the ground floor of a house was found to be seriously decayed five months after construction was completed. The boards showed the longitudinal cracking which is characteristic of attack by this fungus and also bore the superficial white mycelium and a few of the thin brown strands.

On making cultures *Coniophora cerebella* was isolated. As the result of enquiries it was found that the timber used had been wetted by rain before the construction of the floor. The

house was occupied immediately on completion and the floor was at once covered with linoleum. Shortly afterwards the floor was again wetted as the result of leakage of water. In this case ideal conditions for the development of the fungus were present as the wood contained a large amount of moisture, which could not evaporate on account of the impervious covering formed by the linoleum.

A fact of special interest in this case was that the floor had been sometimes wetted by leakage of urine. It has been stated that decay of timber is especially prevalent in buildings such as stables where the wood may become soaked with urine. In a recent investigation by Findlay (1934) it has been shown that treatment of wood with organic nitrogen compounds caused a large increase in the loss of weight due to decay. In the case under consideration it appears probably that the presence of urine hastened the rate of decay.

There is another aspect from which the occurrence of *Coniophora cerebella* is of importance. Falck (1912) and other Continental investigators considered that outbreaks of dry rot are frequently preceded by attack by *Coniophora cerebella* or other fungi which cause decay.

It has been stated in Germany that basidiospores of *Merulius domesticus* cannot attack perfectly sound timber, but that they may do so when the wood has been previously infected with *Coniophora*. It is not clear how far this is true in this country. Falck (1912) has brought forward a large amount of evidence to show that the production of certain organic acids is a predisposing condition for the growth of dry rot in wood and that these substances are produced by the action of *Coniophora* and other fungi.

The results of investigation of two outbreaks of dry rot in Edinburgh are of interest in this connection. In the first, dry rot was found to be present in the uppermost storey of an old house in which the woodwork had become wet as the result of a leakage from the roof gutter. Panelling, floors, and joists were attacked and mycelium and strands of the fungus were present on these and also on the stonework. Fructifications were also developing on the joists. For several years previous no new wood had been brought into the house, and it appeared that the only possible explanation of the outbreak was the assumption that spores of *Merulius* had

been carried in with water from the gutter. Although evidence for the presence of *Coniophora* was searched for none was found.

In the second case dry rot was found to be present in the three uppermost floors of a large building. Some years previously new woodwork had been introduced into the top storey during very wet weather, and the timber used had become very damp. Leakages in the roof had also occurred. On investigation it was found that in addition to *Merulius*, *Coniophora* was present in the woodwork in various parts of the building.

Although no wide conclusion can be drawn from these cases, it appears that in this country the presence of *Coniophora* is not an essential predisposing condition for attack by dry rot.

Lenzites sepiaria has been described on the Continent by Mez (1908) and Falck (1909) as a fungus causing the most serious decay of timber in buildings; it is also recorded as widespread in the United States (Spaulding, 1911), where it often attacks the timber of the roofs of mills (Snell, 1922). It does not appear to be very common in this country, but has been found in Edinburgh producing serious decay of the joists in a building. The timber (*Pinus sylvestris*) showed a very characteristic brown rot in which the partial separation of the annual rings was very marked. Longitudinal and cross shakes were also present; the wood was in a late stage of decay and could be easily crumbled by the finger nail. Hyphae were present in the tracheids, but were in a partially disintegrated condition and showed only few of the characteristic medallion forms. Dark brown hyphae forming the "Cuticularmycel" described by Falck (1909, p. 117) were present on the surface of the separated annual rings.

No fructifications were present, but cushion-like masses of dark brown mycelium had developed on the surface. These masses, which were up to about 1 cm. across and of the same height, were made up of dark brown thick-walled hyphae which have been described by Falck (1909, p. 115) as "Fasermycel." (Fibre mycelium.)

As a result of enquiry it was found that the joist had been in darkness, and this would account for the great development of the masses of fibre mycelium and the absence of fructifications since the latter only develop in the light.

Two species of *Lentinus* are known to cause decay of timber in buildings. These fungi belong to the Agaricaceae, and under normal conditions of illumination produce pilei with centrally attached stipe and radiating gills of the type usually found in the family. When developed in darkness pilei are usually not formed but only the stipes are produced, and these are often much elongated and branched.

Lentinus lepideus has been found in buildings in Edinburgh, developing under feeble illumination. Under these conditions the pileus is often small and may be absent. When present it is often abnormal, bearing irregular outgrowths on which gills are produced. The stipes, whether bearing pilei or not, are frequently branched. This species is distinguished by its yellowish colour and by the production of darker tomentose scales on the stipe and pileus. This species has been found by Buller (1905) to cause the decay of paving blocks consisting of pine heartwood. It is not infrequently found on Scots pine railway sleepers, where it can bring about the decay of the heartwood.

Lentinus adhaerens has been found on the timbering in coal mines in Fife. Here it develops in complete darkness and no pilei are produced. Only much elongated branched stipes are formed. These are frequently forked and have an antler-like appearance. These are at first whitish and tomentose but darken as they become older and are finally dark brown; they may attain the length of a foot.

A somewhat unusual example of growth of a wood destroying fungus was encountered recently when *Polystictus fibula* was found growing on the woodwork in the interior of a saloon motor-car. This species is found occurring not uncommonly on beech trunks as a saprophyte and has also been recorded on elm and oak and on sawn timber.

A very abundant development of fructifications of this fungus occurred some years ago at the Royal Botanic Garden, Edinburgh, on a felled beech trunk. On this occasion it was noticed that young fructifications, while about a $\frac{1}{4}$ inch across varied in colour from bright red to reddish brown, but that this coloration was rapidly lost as development proceeded; when mature, the pore surface of the fructification is of a pale cream colour while the upper surface is slightly yellow or grey. During the early stage they are frequently

cup-shaped and fixed by the centre, and this form is sometimes retained at maturity; usually, however, they become dimidiate, with a resupinate and a shelf-like portion.

In the case of infection on the car the actual wood on which the fungus was growing could not be investigated, but there is little doubt that it was beech. Fructifications developed at the top of the wind-screen, the moisture necessary for their development being supplied by a slight leakage in the roof. Cultures were readily obtained both from basidiospores and also from small portions of the fructification. The fungus grew readily on malt agar, producing an abundant white mycelium on which no spores were developed.

Cultures on sterilised beech blocks produced fructifications within three months. Some of these were reddish and cup-shaped at first but later became resupinate with a white pore surface; in these a reddish-brown border persisted around the fructification.

Examination of the infected blocks after ten months showed that little decay had taken place and the wood was on the whole still sound and hard. Numerous hyphae were present especially in the vessels.

There appears to be little doubt that the wood used in the construction of the car was already infected. This could quite easily occur since the fungus appears to have little effect on the wood in the early stages of its development.

The decay of wood caused by *Trametes serialis* is not uncommon in North America and has recently been described in this country (Cartwright, 1930) in the case of spruce timber imported from Canada. Up to the present it does nor appear to have been recorded in buildings in this country. A outbreak was investigated in Edinburgh in 1929, in which joists, supporting a concrete floor, had become seriously decayed as the result of attack by this fungus, resulting in a slight sinking of the flooring. The space below the flooring, about two feet in depth, was unventilated and partly occupied by hot-water pipes; in consequence the temperature was unusually high. This fact is of considerable interest as the optimum temperature for the growth of this fungus, 28° C. (Snell, 1922), is high compared with that of *Merulius domesticus* (about 22° C.). Numerous plates and strands of white mycelium, with a characteristic smooth and shining appearance, were present on

the surface of the wood but no fructifications were found. As a result of examination it was found that the timber was spruce and that numerous hyphae were present in the tracheids. Some of these showed the characteristic "medallions"—structures which appear to consist of a double clamp-connection.

This fungus is characterised by the production of conidia; these were found in the tracheids and were abundantly produced when the fungus was obtained in culture.

On enquiry it was ascertained that the flooring had been constructed shortly after the close of the war. No information could be obtained regarding the source of the timber. It appears likely, however, that the place of origin was North America, as at that time supplies of European spruce were difficult to obtain.

Probably the fungus was already present in the timber when used in the construction.

Trametes serialis is known to exist in a viable condition in timber for long periods (Hubert, 1931). In this case the actual condition determining the outbreak was apparently brought about by leakage from a hot-water pipe.

In conclusion, the value of cultures in the identification of wood-rotting fungi must be emphasised, especially in those cases where little or no mycelium is present on the surface of the wood.

It is generally admitted that it is not possible to identify *Merulius domesticus* with certainty merely from the examination of hyphae in the wood tissues. Even where characteristic structures occur in the mycelium, such as the "finger hyphae" in *Coniophora cerebella*, the "medallions" of *Lenzites* sp., and the conidia in *Trametes serialis*, it is inadvisable to make a definite identification until cultures prepared from the wood have been examined.

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Variations in an 8-Cell Group.

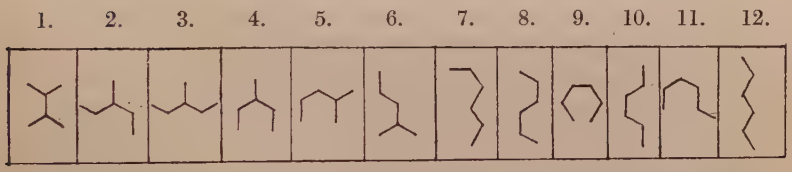
By D. H. Welch, B.Sc.

(Read 18th April 1935.)

This paper will, for convenience, only deal with groups of eight cells lying in the same plane and having a common boundary. Such a group would be produced by the segmentation of a flat, discoidal cell by radial walls.

Professor D'Arcy Wentworth Thompson (1) has shown that, in virtue of Errera's Law (2), the Law of Minimal Areas (1, *a*) and Lamarle's Law (3), such a group may be arranged in twelve ways, each arrangement being represented by the internal skeleton, *i.e.* the collection of internal partitions or "connecting lines." Fig. 2 represents the internal skeleton of fig. 1, and the skeletons of the twelve types are set out in Table I., the numbering being arbitrary.

Table I.—Types of Skeleton.



The object of the work was to find out if all these types occurred in Nature, and if so, in what relative numbers. *Lavandula vera* DC. was selected for plant material in virtue of its glandular hairs, each with a flat, discoidal, 8-celled head, and *Rana temporaria* for animal material in virtue of its easily studied eggs. These were examined at the 32-cell stage when an 8-cell group had developed from each quadrant. It will be noticed that in Lavandula (fig. 1) the partitions do not meet at equal angles as they do in the frog's egg (fig. 3). This is because in Lavandula the cell-walls become rigid before segmentation is complete, whereas in Rana the walls remain supple and pliable, if not exactly fluid.

Table II.

Type No. . . .	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
Percentage occurrence in Lavandula	5·5	18	15	8	11	11	24	7·5	0	0	0	5
Percentage occurrence in Rana	2	16	9·5	12	13	13·6	9·5	7·8	1·2	3·8	4·1	7·5

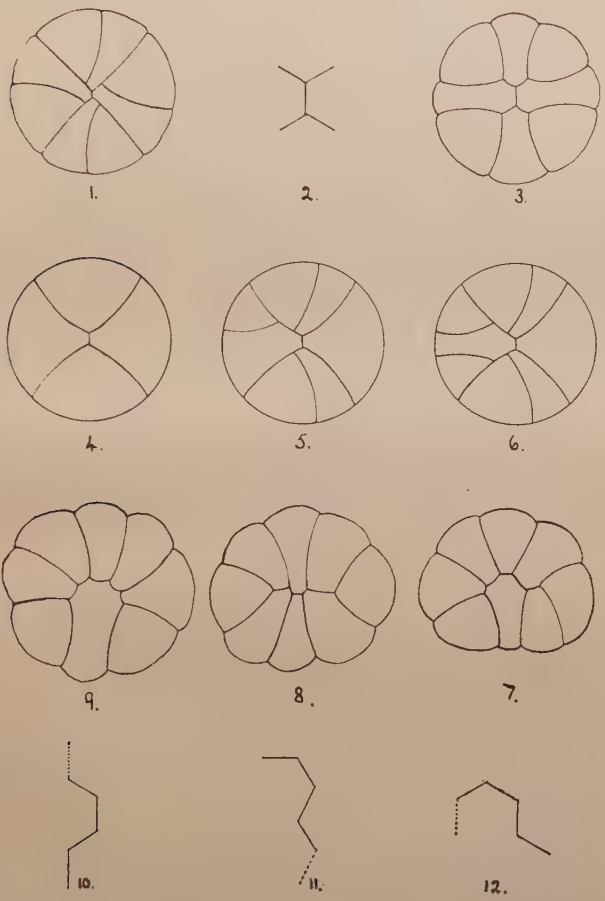
Table II. shows the percentage occurrence of the twelve types in the two examples taken. In developing frogs' eggs all twelve types are found, but in Lavandula three types are missing. This difference may be explained thus: In the missing types (9, 10, and 11) the skeleton is such that it can only be formed by the lagging behind of one quadrant and the premature division of one octant, as shown in figs. 4, 5, and 6. Now this is quite possible in Rana (figs. 7, 8, and 9), where each cell goes on dividing for a long time, but in Lavandula, where there are only eight cells in the head, it is unlikely that an octant will ever divide, as 9–16 cells might be so formed. It would be interesting to know if such a gland, with more than eight cells, has been found. The reason why the octants in Lavandula never divide is well outside the scope of this work, but the fact remains and will explain the lack of these three types.

Most of these types have mirror images but, though these were seen to occur, statistics were not taken.

Apart from the three missing types, there is a close correlation between the percentage occurrences in Rana and Lavandula. The least common types in Rana are 1, 12, and 8, and in Lavandula 12, 1, and 8 respectively. The most common types in Lavandula are 7 and 2, whereas in Rana 2 is common but 7 is not. This may be explained thus: It will be noticed that types 10 and 11 are easily derived from type 7 as shown in figs. 10, 11, and 12. Now it has already been explained that types 10 and 11 are "freaks" due to irregular development, and it is easy to suppose that these types (10 and 11), are potential 7's "gone astray." If they are treated as such, and grouped along with 7, the percentage occurrence becomes 17·4, thus bringing Rana into line with Lavandula.

This explanation, for reasons not far to seek, must remain hypothetical, but one point of importance does arise. The correlation between these widely different examples is close

enough to warrant further work being done on the subject, so that the laws governing the occurrence of these variations may be further cleared up. It is likely that the type occurring



most frequently is the most stable system. In the developing frog's egg, where the walls are almost fluid, these will slide on one another until the most stable system is obtained. This, no doubt, explains in part the "working" of such a developing egg, as if the whole were a seething mass of bubbles.

Summary.

1. Professor D'Arcy Wentworth Thompson has shown that there are twelve theoretical variations in the arrangement of a group of eight cells, lying in the same plane and enclosed by a common boundary.

2. All these twelve types have been found in the developing eggs of the frog, while three types are missing from the glandular hairs of Lavandula, owing to the inability of the octants to divide.

3. There is close correlation between the percentage occurrence of the types in Rana and Lavandula, especially if types 10 and 11 are considered as potential 7's which have not developed properly.

4. It is suggested that further work might elucidate the laws governing these variations.

The author wishes to take this opportunity to thank Professor D'Arcy Wentworth Thompson for suggesting the work, Professor R. J. D. Graham for encouragement and help, and the Carnegie Trust for a research grant.

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The Floral Mechanism of Saurauja subspinosa Anth. By Ernest G. S. Brown, B.Sc.

(Read 18th April 1935.)

Introduction.

Saurauja subspinosa Anth. (1). Ternstroemiaceae.

The genus *Saurauja* consists of trees and shrubs found in the tropical and sub-tropical regions of Asia and America. Specimens of *Saurauja subspinosa* were collected by Forrest during 1924–25 in N.E. Upper Burma, and from seed obtained by this collector one plant of the species is now under cultivation in the Royal Botanic Garden, Edinburgh. It was from this plant that material was obtained and observations made for the following investigation. The plant takes the form of a woody shrub, branching freely from near the base, and reaching a height of about ten feet. The leaves are large and lanceolate, having a spiny serrulated margin, and are produced spirally towards the ends of the branches. The inflorescences are produced in the axils of the upper leaves, each inflorescence bearing 15–20 pale rose-pink flowers.

Floral Description.

Inflorescence.—The inflorescence is axillary, consisting of a peduncle which gives rise to axillary cymes in a racemose manner. Each inflorescence produces 5–7 axillary cymes. Each cyme rises in the axil of a bract and consists of 3–5 flowers. The flowers are borne on pedicels, each flower being subtended by a bract and bearing two lateral bracteoles.

Receptacle.—Flattened and disc-shaped.

Flower.—Hermaphrodite and regular, about half an inch in diameter.

Calyx.—Five sepals which are strongly imbricated, orbicular, concave, and translucent.

Corolla.—Five petals alternating with the sepals. The petals are united at the base to form a gamopetalous corolla, with the free parts of the petals strongly imbricated in the

bud. The corolla is pale pink in colour, except in the inside of the cup formed by the fusion of the petals, which is dark red. This gives the flower a very conspicuous appearance.

Androecium.—The stamens are almost invariably fifty in number and adhere to the base of the corolla. When the fused petals are separated it is found that the stamens tend to be arranged in bundles opposite the petals, and a hand dissection of the flower shows that the stamens arise by splitting. The stamens develop centrifugally. The filament is inserted about one third of the way up the anther, which is inclined outwards and dehisces by apical pores.

Gynoecium.—The ovary is globose in shape, superior, syncarpous with five cells, the cells alternating with the petals. The styles are five in number, fused at the base but free spreading towards the apex. The stigmata are capitate. The ovules, which are anatropous, are numerous in each cell, attached to an axile placenta.

Nectary.—There is no definite nectary present in the flower, but nectar-secreting tissue is found at the base of the corolla, inside, partly hidden by the stamens. The flowers have a faint, sweet scent.

Development of the Flower.

In order to trace out the development of the flower parts, young flower buds of various ages were obtained from the plant. The buds were fixed for twenty-four hours in Bles Fixing Fluid, and then graded into various sizes, the age of the buds being assumed to be proportional to their size. They were then taken through alcohol into xylol, embedded in paraffin, and sectioned by microtome. Both transverse and longitudinal sections, in complete series, were cut of buds in all the available sizes. The sections were stained by the iron-alum haematoxylin method, and, with the aid of a camera lucida, outline drawings were made of the various stages of development found.

Calyx.

The ordinary vegetative leaves of the plant are arranged spirally having a phyllotaxis of $\frac{2}{5}$, and this arrangement is

carried into the bracteoles and sepals. The bracteoles and sepals thus arise in a spiral manner, the fourth sepal arising directly above the first bracteole, and the fifth sepal directly above the second bracteole. As in practically all other flowers which are pentamerous and in which two bracteoles are typically present, the sepals arise in a very definite manner (5, *a*). The position of the first bracteole is to the left of the median line, and the second bracteole arises slightly higher up, laterally opposed to the first. The first sepal is anterior and to the left of the median line. The second sepal is posterior and distinctly median. The third sepal is again anterior but

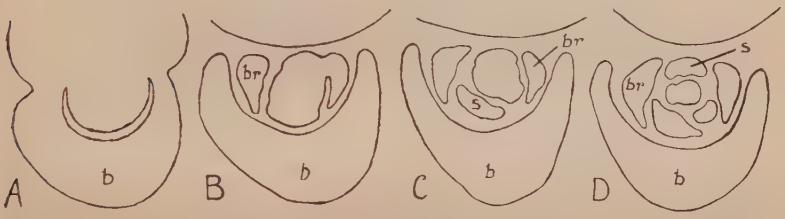

FIG. 1.—A series of four transverse sections taken through a young flower bud still in the stage of sepal formation. × 40.
b = bract, br = bracteole, s = sepal.

to the right of the median line. The fourth and fifth sepals are lateral or nearly so, and arise to the left and right respectively of the median line. This appears to be the state of affairs in practically all pentamerous flowers in which two bracteoles are typically present, as opposed to the condition where the bracteoles are absent and the first sepals arise laterally to take the place of the bracteoles. The sepals in this flower, being spiral in origin, naturally imbricate in the manner known as quincuncial prefloration (2).

The manner in which the bracteoles and sepals arise is shown very clearly in fig. 1. This figure shows four transverse sections taken from a complete series, from base to apex, of a bud which has developed only to the extent of producing its bracteoles and the first three sepals. In fig. 1, D, the position of the fourth sepal is indicated by a small protuberance, which represents in section the first differentiation of the sepal. The production of the sepals in a spiral manner is clearly shown also

in fig. 2, A, which is a longitudinal section of a young bud still in the stage of sepal formation.

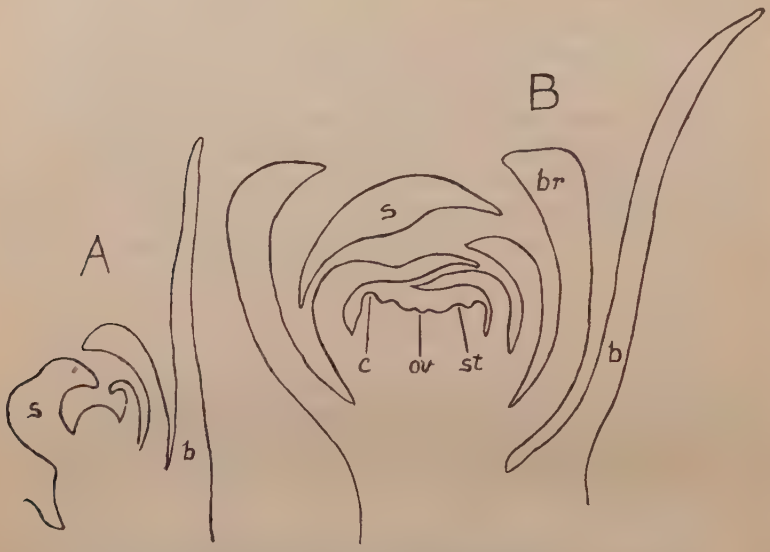

Fig. 2.—Young flower buds in longitudinal section. × 40.
A. Flower bud still in the stage of sepal formation.
B. A further advanced stage showing the first differentiation of petals, stamens, and ovary. This section was not cut through the median plane, and the two bracteoles are seen in section.
b = bract, br = bracteole, s = sepal, c = corolla, st = stamens, ov = ovary.

Corolla.

There appears to be a distinct interval in time between the production of the sepals and the petals, as fig. 2, A, shows a bud with sepals relatively well formed before any indication of petals can be made out. Fig. 2, B, shows a longitudinal section in which the first indication of the petals may be seen. In this figure the petals appear to arise from the same level and show no sign of spiral arrangement. The five petals alternate with the sepals and are formed as a true cyclic whorl. This is well seen in fig. 3, A, in which the petals are quite free and discrete in transverse section. The petals fuse at the base at a very early stage, and the bud from which fig. 3, A, was taken was the only one obtained showing the petals free and discrete. The series of sections obtained from this bud gives reasonable evidence of the true cyclic arrangement of the

petals, which by fusion at their base give rise later to a gamopetalous corolla. As the petals enlarge, the free upper parts become imbricated by sliding growth of their edges as they extend laterally. This imbrication may follow the same arrangement as that invariably found in the sepals, and this

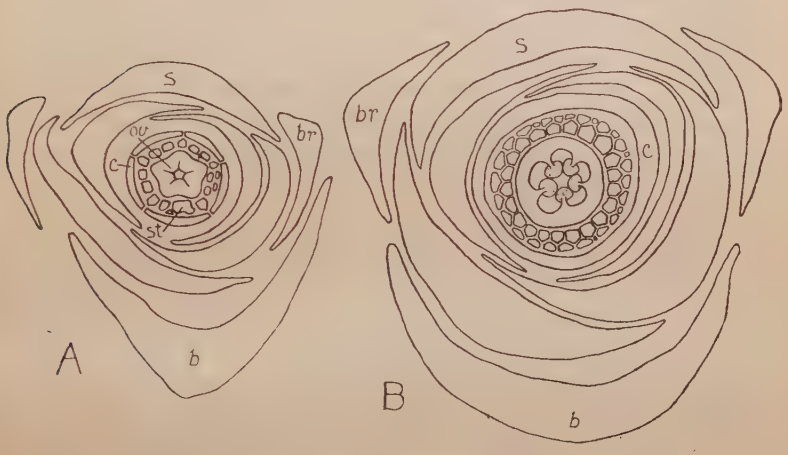

Fig. 3.—Flower buds in transverse section. × 35.
A. Stage showing petals free and discrete.
B. A further advanced stage showing the petals united and the ingrowths of the ovary wall pushing in to meet and fuse at the centre.
Lettering as in fig. 2.

is generally found. But this method of imbrication is not invariable in the case of petals, and the arrangement known as bilateral prefloration (2) is sometimes found.

Androecium.

An examination of the mature flower reveals that the stamens, which are numerous, arise centrifugally and show evidence of splitting having taken place. In many cases the complete separation of splitting stamens has not been effected, and one may find as many as three stamens of different sizes all having a common filament at the base. When the petals of the fused corolla are separated carefully and examined, one is able to make out a faint indication of the stamens being arranged in bundles opposite the petals. A single stamen is found opposite each sepal. Another point of interest is that numerous counts revealed that the number of stamens in the flower is almost invariably fifty.

The stamens arise quite soon after the first indication of the petals, as seen in fig. 2, B, which shows the first indication of the stamens as small protuberances, while the petals have not advanced much beyond the same stage. In cutting transverse sections, it was expected that a young enough stage would be found to show ten stamens in two whorls of five. Numerous buds, which, judged by size, would probably be at this stage, were sectioned. The youngest stage found showing stamens, however, had developed to the extent of having fifteen, and fig. 3, A, represents a drawing of one section in the series obtained from this bud. In this section

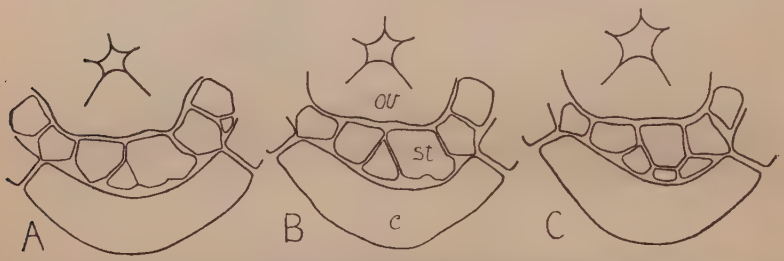

FIG. 4.—A series of three transverse sections, from base to apex, of a young flower bud, centred on the region opposite a petal, to show the splitting of the stamens. × 88. Lettering as in fig. 2.

there are fifteen stamens of which five are definitely placed exactly opposite the sepals, and the others are in pairs, one pair opposite each petal. The stamens opposite the sepals appear to be placed rather farther out than the others, and presumably arose first as a whorl of five. It is probable that the other ten stamens may be accounted for, by assuming that they arose by the splitting of five stamens, originally opposite the petals, which formed a whorl farther in than the sepal stamens. The fact that the carpels or cells of the ovary are opposite the sepals renders this suggestion all the more probable, as this leads to a regular alternation of five sepals, five petals, five outer stamens, five inner stamens, and five carpels; the state of affairs in diplostemonous flowers.

The series of sections from which fig. 3, A, was taken are the only ones showing the five sepal stamens in definite position. This definiteness of position of these stamens is lost later by the rapid multiplication of the stamens and the fusion of the

petals. In this way the series of sections obtained from this bud was used to produce evidence of the splitting of the stamens. Fig. 4 shows a series of three transverse sections taken from the base to the apex of this bud, centred on the region opposite a petal, under high power magnification. This series shows quite clearly that the stamens multiply by splitting, and that the splitting takes place from the stamens opposite the petal.

In older buds, both in transverse and longitudinal section, abundant evidence of splitting may be found. The splitting

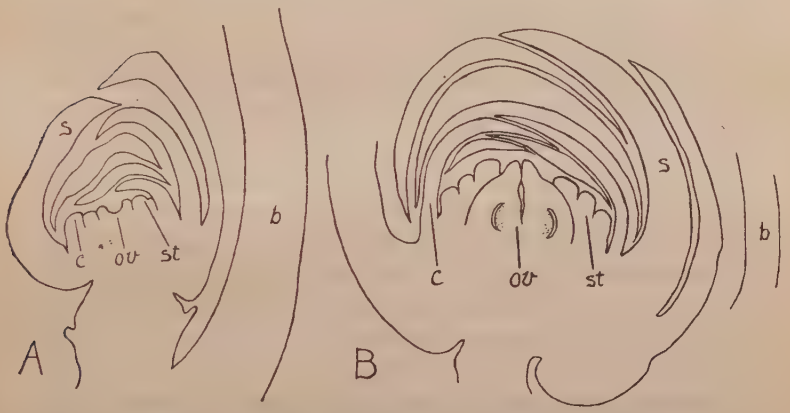

Fig. 5.—Flower buds in longitudinal section. × 32.
A. Early stage in the development of the stamens and ovary.
B. Further advanced stage showing the stamens splitting, and the ovary before complete fusion has taken place at the centre.
Lettering as in fig. 2.

takes place very early in the development of the stamens, as seen in fig. 5, A, which shows indication of splitting in the stamen to the right, while the stamen is still a small undifferentiated protuberance. The facts that the splitting takes place so early in development, that multiplication gives rise to numerous stamens which are closely pressed together in a limited space, and that splitting always gives rise to perfect stamens with four pollen sacs, render it difficult to trace back the origin of the stamens in the older sections.

Thus the evidence regarding the origin of the stamens must be looked for in the series of sections from which fig. 4 was taken. An examination of this series failed to reveal any splitting on the part of the stamens opposite the sepals. Such

evidence seems to indicate that the stamens are formed originally in two whorls of five, the outer and first formed whorl being opposite the sepals, and the inner, second formed whorl, opposite the petals. Evidence from the same source indicates also that the numerous stamens arise by the splitting of the petal stamens. This may account for the indication of bundles of stamens opposite the petals in the mature flower, and also for the regularity in the number of stamens.

Gynoecium.

The ovary arises very soon after the stamens, and the first indication of its differentiation is found in such a young stage as that represented in fig. 2, B. In this section the first indication of the ovary can be recognised as a small depression in the centre of the receptacle, caused by the first rising up of the future ovary wall. The next stage in the development of the ovary is seen in fig. 5, A. As this is a longitudinal section it is impossible to interpret the exact nature of the ovary. However, this section is one taken from a complete series through the bud, and an examination of this series leads one to regard the ovary as taking the form of a small cup. The ovary in transverse section, as seen in fig. 3, A, represents the next stage in development, in which the ovary wall forms five protuberances on the inside, which grow inwards to the centre. These protuberances are opposite the petals. It is quite possible that the ovary in a younger stage than represented in fig. 5, A, might arise as five distinct carpellary growths, which fuse very early to form a small cup, and that the ingrowths to the centre, seen fig. 3, A, represent the lines of fusion of the carpels.

The next stage in the development of the ovary is seen in fig. 3, B, which is one of a series of transverse sections taken through a young flower bud. This series shows that the ingrowths from the inside of the ovary wall meet at the centre and fuse from below upwards. Fig. 3, B, reveals also the fact that the placentae are formed very early, being present before fusion takes place at the centre to form the five cells of the ovary. The ovary as seen in a section taken through the apex of this bud is identical with the condition found in the entire interior of the ovary in a younger bud. Fig. 5, B, is a drawing showing the ovary in longitudinal section at about

the same stage as seen in the transverse section of fig. 3, B. The formation of the placentae before fusion is complete at the centre can again be made out. In a slightly further advanced stage in the development of the ovary fusion at the centre is almost complete, and the first differentiation of the styles may be seen. After fusion at the centre is completed to form the five loculi, the ovules are produced on the placentae in each loculus and we thus arrive at the condition found in the mature flower. The styles are formed opposite the sepals, and their canals are continuations from the loculi of the ovary which represent the five original carpels.

Development of the Inflorescence.

In the young inflorescence the peduncle is almost erect, and each axillary cyme is enclosed in a green bract. As the inflorescence enlarges, the bracts enclosing the cymes open out to reveal the young flower buds, which are also green. The green colour of the inflorescence at this stage indicates photosynthetic activity, which is facilitated by the erect position of the peduncle, allowing greater freedom of light. Each flower is subtended by a green bract and bears two lateral green bracteoles, and later a short pedicel is developed. The bracts subtending the cymes are shed, without withering, just as the sepals of the terminal flower in the cyme part to reveal the pink petals. Up to this point the sepals are green in colour, but they now gradually lose their green colour, turning white and translucent. About 10–14 days after the shedding of the bract subtending the cyme the terminal flower opens. Then the flower bract and bracteoles quickly wither and fall to the ground; each flower in the inflorescence loses its bract and bracteoles as it opens.

As the flowers are developing the peduncle gradually swings down from its erect position and spreads horizontally. At the same time the pedicels all curve downwards, so that all the flowers after opening face downwards towards the ground. The stamens come to maturity first, the innermost stamens being ready to discharge their pollen as soon as the flower opens. The pollen is discharged from the anthers by means of apical pores. After the pollen has been shed, the corolla with the adhering stamens falls to the ground in one piece, and

does not wither on the plant. The time from the opening of the flower till the corolla is shed is 5–7 days. After the corolla has been shed the sepals close round the ovary and completely cover it except at the apex, where the five free styles protrude.

Up to this point the stigmata do not appear to be receptive. The flower pedicels now turn slowly round through 180° to become erect, in 3–5 days. It is during this gradual turning of the pedicel that the stigmata become receptive. The stigmata of the flower, now pointing upwards, show a glistening and mucilaginous surface. If fertilisation does not take place, the sepals open out again and wither, the ovary shrivels and turns brown, and with the pedicel fall to the ground. If fertilisation does take place, the sepals remain firmly closed round the ovary.

While the flowers are being pollinated the peduncle of the inflorescence gradually turns upwards to assume an erect position again, with the result that, after pollination of the inflorescence as a whole, the peduncle stands straight up again, carrying the young fruits in an erect position. The sepals remain firmly closed round the young fruit with the five free styles protruding at the top. The return of the peduncle to an erect position places the young fruits in a more favourable position for further development. The movements of the peduncle, and of the flower pedicels, suggest some sort of adaptation for pollination.

Pollination.

In the case of the plant concerned, it was observed that a very small number of fruits were formed relative to the amount of flowers produced. This suggests that either the pollination mechanism is not working very efficiently, or that the plant is self-incompatible to a great extent. The flowers have a sweet scent and are very conspicuous in colour. The corolla produces nectar at its base, the nectar-secreting tissue being partly hidden underneath the stamens. In the young flower the sweet scent and presence of nectar will attract insects, which will carry away pollen after visiting the flower. Flowers at this stage, however, do not have receptive stigmata. The stigmata of the flower become receptive only after the shed-

ding of the corolla and stamens, and the turning upwards of the pedicel. Thus the flower in which the stigmata are receptive does not possess anything which would be likely to attract the insects, and bring about the direct pollination of the stigmata.

When the flower pedicel turns upwards after the shedding of the corolla and stamens, the now receptive stigmata are placed in a very favourable position to receive pollen from the other flowers higher up, which are still facing downwards, on the same plant or on neighbouring plants. It is probable that the insects, visiting the flowers in search of nectar, will cause the dehiscence of the anthers and the shedding of the pollen by disturbing the stamens, as the nectar is found at the base of the corolla, partly underneath the stamens. In this way the visitation of the insects to the flowers would cause the downfall or spread of pollen. This would bring about the pollination of the receptive stigmata of flowers which are standing erect, lower down on the same plant or on neighbouring plants.

It is more than probable that cross-pollination would be effected in this way, as it would only be in the absence of air currents that the pollen would fall directly down. The dehiscence of the anthers by apical pores, and also the fact that the earliest flowers are produced on the lowermost branches, tend to favour this explanation of the pollination mechanism. The low percentage of fruits produced on the plant under observation may be due to the fact that the proper insect is absent, or that the plants are naturally self-incompatible to a great extent.

Fruit.

The fertilised ovary or young fruit retains the sepals closed round it with the free styles protruding at the top. As development takes place, the peduncle and pedicels carrying the fruits in an erect position tend to become red in colour. This is most marked in the cases where the peduncle gets clear of the leaves and is fully exposed to the light. The exposed part of the fruit also tends to take on a reddish tinge, and the fruit, enlarging in size, swells up, pushing out the enclosing sepals. At the same time, changes are going on inside the fruit, resulting in the formation of a mucilaginous

pulp in each loculus. Embedded in this pulp are numerous seeds which take on a dark brown colour and become quite hard. Thus the mature fruit takes the form of a berry, containing numerous small seeds, in five chambers, embedded in a mucilaginous pulp. This appears to be quite typical of the fruit form in the genus.

Discussion and Conclusion.

To sum up, the flower of *Saurauja subspinosa* is regular and pentamerous, showing a regular alternation of its sepals, petals, outer stamens, inner stamens, and carpels. The sepals are spiral in origin and arrangement, the other whorls are cyclic. The flower is fundamentally diplostemonous. The number of stamens is increased, almost invariably to fifty, by the splitting of the inner stamens which are opposite the petals. The fact that the multiplication of the stamens is brought about by the splitting of the original whorl opposite the petals tends to give the appearance of bundles of stamens opposite the petals in the mature flower. This is rather obscure in *Saurauja subspinosa*, as the numerous stamens are closely pressed together in such a small flower, and the corolla is decidedly gamopetalous.

It is possible to trace an evolutionary progression among certain numbers of Ternstroemiaceae with regard to the character of the androecium. The primitive condition in this progression is that in which the stamens are ten in number, forming two whorls, and this is exemplified by *Visnea* (4). Passing from this we come to the condition found in *Saurauja subspinosa*, in which ten stamens are again present in two whorls, but numerous stamens are produced by the splitting of the petal-stamens. In this case the sepal-stamens are present but do not split. The suppression of the sepal-stamens forms the next step in the progression. This is found in *Saurauja lanceolata* (3), *Kielmeyera* (5, *b*), and *Gordonia* (4), which have numerous stamens produced by the splitting of five original petal-stamens, the sepal-stamens being suppressed. In this case the arrangement of the stamens in bundles opposite the petals is more distinct. In this general trend the efficiency of the stamens produced by the splitting of the petal-stamens would lead to the suppression of the other whorl, opposite the sepals. The formation of numerous

stamens by the splitting of five original petal-stamens would lead to the arrangement of bundles of stamens opposite the petals.

It has been stated by Warming (5, *c*), and is generally accepted, that in Ternstroemiaceae the numerous stamens are always formed by the splitting of a small number, a true spiral arrangement never being found. Many other forms in Ternstroemiaceae, such as *Thea*, have numerous stamens which appear to be cyclic, but show no tendency to be arranged in bundles. In the absence of any investigation it may be suggested that this condition has been derived also from a type with ten stamens, by the splitting of all the stamens.

The inflorescence of *Saurauja subspinosa* shows an interesting series of movements correlated with the pollination of the plant, and an explanation of the pollination mechanism has been offered. The floral development of this plant has been worked out, but as no work of a similar nature has been done with any other plant in this family it is impossible to draw any general comparisons.

In conclusion the author wishes to express his indebtedness to Professor Sir W. Wright Smith for his valuable supervision of the work and criticism of the manuscript.

Summary.

This paper contains a detailed description of the flower of *Saurauja subspinosa* Anth.

The development of the flower parts is described also in detail.

This is followed by a description of the inflorescence, the development of which is closely associated with the pollination.

A brief description of the fruit precedes the discussion and conclusion, in which the development of the stamens forms the main part.

References.

(1) Anthony, J.: Notes from the Royal Botanic Garden, Edinburgh, xv (1927), 244.
(2) Church, A. H.: Types of Floral Mechanism, Part 1 (1908), 186.
(3) De Candolle, A. P.: Memoire sur la Famille des Ternstroemiacées et en particulier sur le genre Saurauja. 1820.
(4) Engler-Prantl: Naturliche Pflanzenfamilien, iii Teil, 6 Abteilung, 177.
(5) Warming-Potter: A Handbook of Systematic Botany (1920), (*a*) p. 335; (*b*) p. 415; (*c*) p. 406.

Survey of the Marine Algae of the Coast of Fife.

By D. N. Lowe, M.A., B.Sc.

(Read 13th June 1935.)

The marine algae of the Firth of Forth have been studied by Dr. James M'Bain and G. W. Traill. M'Bain's survey was published in 1862 (1). Traill's first list was published in 1855 (2), and his second in 1889 (3). So far as the coast of Fife is concerned, these records are confined to stations near Elie, and there is no published account of further surveys during the past forty-six years.

The work now being reported was undertaken with a view to extending the survey from Elie to St. Andrews, and was suggested by a bequest to the Department of Botany, St. Andrews University, by the late Mr. J. A. Terras of Crail—a Fellow of the Botanical Society of Edinburgh. The bequest took the form of:

(*a*) A collection of algae, preserved and pressed, made by Mr. Terras from the area Crail, Fife Ness, and Balcomie, in the winter and spring of 1930–31, and the following summer and autumn.

(*b*) A quantity of meticulous notes giving observations from week to week on the specimens collected.

M'Bain listed 104 spp. in 59 genera, Traill 177 spp. in 82 genera, and Terras, whose work was prematurely stopped by his death, had noted 100 spp. in 73 genera. Careful examination of the material, however, necessitated some revision of this computation, and the collection was found to contain 107 species in 71 genera, 10 spp. in 8 genera being rejected, and 17 spp. in 12 genera being added. These are:

Acinetospora pusilla Born.
Ahnfeldtia plicata Fries
Alaria esculenta Grev.
Ascophyllum nodosum Stackh.
Asperococcus echinatus Grev.
Bangia fusco-purpurea Lyngb.
Callithamnion arbuscula Lyngb.

Callithamnion Brodiaei Harv.
,, *byssoides* Arn.
,, *fasciculata* Lyngb.
,, *granulatum* Ag.
,, *Hookeri* Ag.
Callophyllis laciniata Kütz.
Calothrix fasciculata Ag.
Castagnea virescens Derb. et Sol.
Catenella opuntia Grev.
Ceramium acanthonotum Carm.
,, *arborescens* Ag.
,, *diaphanum* Roth
,, *fruticulosum* Kütz.
,, *rubrum* Ag.
Chaetomorpha melagonium Kütz.
Chaetopteris plumosa Kütz.
Chondrus crispus Lyngb.
Chorda Filum Lamour.
Chordaria flagelliformis Ag.
Cladophora albida Huds.
,, *arcta* Kütz.
,, *flexuosa* Harv.
,, *lanosa* Kütz.
,, *rupestris* Kütz.
,, *sericea* Kütz.
,, *spongiosa* Kütz.
Corallina officinalis Linn.
Cruoria pellita Fries
Cystoclonium purpurascens Ag.
Dasya coccinea Ag.
Delesseria sanguinea Lamour.
Desmarestia aculeata Lamour.
Dictyosiphon foeniculaceus Grev.
Dictyota dichotoma Lamour.
Dilsea edulis Stackh.
Dumontia filiformis Grev.
Ectocarpus confervoides Le Jol.
,, *fasciculatus* Harv.
,, *littoralis* Lyngb.
,, *tomentosus* Lyngb.
Elachistea fucicola Fr.

Enteromorpha clathrata Ag.
,, *compressa* Grev.
,, *marginata* Ag.
,, *minima* Naeg.
Fucus platycarpus Thur.
,, *serratus* Linn.
,, *vesiculosus* Linn.
Furcellaria fastigiata Grev.
Gelidium corneum Lamour.
Gigartina mamillosa J. Ag.
Griffithsia setacea Ag.
Halydris siliquosa Lyngb.
Himanthalia lorea Lyngb.
Isthmoplea sphaerophora Kjellm.
Laminaria digitata Lamour.
,, *saccharina* Lamour.
Laurencia pinnatifida Lamour.
Leptonema fasciculatum Reinke
Litosiphon Laminariae Harv.
Lomentaria articulata Ag.
,, *clavellosa* Gaill.
Melobesia polymorpha Harv.
Membranoptera alata Kylin
Microcoleus chthonoplastes Thur.
Myrionema punctiforme Harv.
Myriotrichia filiformis Harv.
Nitophyllum laceratum Grev.
Odonthalia dentata Lyngb.
Pantoneura angustissima Kylin
Phycodrus rubens Batt.
Phyllitis Fascia Kütz.
Phyllophora Brodiaei J. Ag.
,, *membranifolia* J. Ag.
Pilayella littoralis Kjellm.
Plocamium coccineum Lyngb.
Plumaria elegans Schmitz
,, *pluma* Stackh.
Polyides rotundus Harv.
Polysiphonia Brodiaei Grev.
,, *elongata* Grev.
,, *fastigiata* Grev.

Polysiphonia fibrata Harv.
,, *nigra* Batt.
,, *nigrescens* Grev.
,, *urceolata* Grev.
Porphyra laciniata Ag.
Prasiola marina Crouan
Ptilota plumosa Ag.
Punctaria plantaginea Grev.
Ralfsia verruscosa Harv.
Rhodochorton floridulum Naeg.
Rhodomela lycopodioides Ag.
,, *subfusca* Ag.
Rhodymenia palmata Grev
Sphacelaria cirrhosa Ag.
,, *olivacea* Ag.
,, *radicans* Harv.
Ulothrix flacca Thuret
,, *isogona* Thuret
Ulva latissima Linn.

By comparison with previous surveys it is seen that ten species may be added to the algal flora recorded for the coast of Fife. These are:

Acinetospora pusilla Born. (*Ectocarpus pusillus*, Harv.)
Callithamnion byssoides Arn.
Ceramium arborescens Ag.
,, *fruticulosum* Kütz.
Cladophora flexuosa Harv.
,, *sericea* Kütz. (*Conferva laetevirens*, Dillwyn)
Enteromorpha minima Naeg.
Microcoleus chthonoplastes Thur.
Pantoneura angustissima Kylin (*Delesseria angust* Griff.)
Plumaria elegans Schmitz (*Ptilota sericea* Harv.)

Of these, nine are described by Newton (4) as "not uncommon, widely distributed," while *Acinetospora pusilla* is "rather rare, widely distributed," and *Ceramium fruticulosum* "rare, found in Devon, Dorset, Northumberland."

In his second survey (3) Traill has said: "The dates given for fructifications and duration of species are necessarily approximate in certain cases, varying according to the maturing influence of the seasons," and, making this allowance, Terras's

observations agree, in the main, with Traill's, but there are several startling differences worth noting. These may be briefly tabulated.

	Traill.	Terras.
Ahnfeldtia plicata	Fruit early in winter.	Fruit as late as 9th April. Roome Bay.
Alaria esculenta	Fruit early in winter.	Fruit as late as 23rd March. Staples Reef.
Callophyllis laciniata	"Capsules" in spring.	Beginnings of spore formation on 8th December. Staples Reef.
Ceramium acanthonotum	Fruit winter and spring.	Tetrasporangia and cystocarps on 9th July. Pans Reef.
Chondrus crispa	Fruit spring and winter.	Numerous plants with cystocarps gathered at low water of 29-foot tide from July on. Roome Bay.
Cladostephus spongiosus	Fruit in winter.	None observed all winter. First seen on 6th March. Staples Reef.
Membranoptera (*Delesseria*) *alata*	Fruit March, April, and May.	Tetrasporangia and cystocarps abundant on 2nd February. Washed ashore. Roome Bay.

The following list of algae of the Kinkell coast of St. Andrews Bay has been compiled from three sources: (*a*) Herbarium collection by the late Professor M'Intosh, (*b*) Herbarium collection by the late Dr. Wilson (both of St. Andrews), and (*c*) collections made in the spring of 1935.

Ahnfeldtia plicata.
Ascophyllum nodosum.
Callithamnion fasciculata.
,, *Hookeri.*
Callophyllis laciniata.
Ceramium diaphanum.
,, *rubrum.*
Chaetomorpha melagonium.
Chondrus crispus.
Chorda Filum.
Chordaria flagelliformis.
Cladophora rupestris.
,, *sinuosa.*
Corallina officinalis.
Cystoclonium purpurascens.
Delesseria sanguinea.
,, *sinuosa.*
Desmarestia aculeata.
Dictyota dichotoma.
Dilsea edulis.

Dumontia filiformis.
Elachistea fucicola.
Enteromorpha compressa.
,, *intestinalis.*
Fucus serratus.
,, *vesiculosus.*
Furcellaria fastigiata.
Halydris siliquosa.
Himanthalia lorea.
Laminaria digitata.
,, *saccharina.*
Laurencia obtusa.
,, *pinnatifida.*
Leathesia tuberiformis.
Lomentaria articulata.
,, *clavellosa.*
Melobesia polymorpha.
Membranoptera alata.
Nemalion multifidum.
Odonthalia dentata.
Pelvetia canaliculata.
Phyllophora rubens.
Plocamium coccineum.
Polysiphonia Brodiaei.
,, *elongata.*
,, *fastigiata.*
,, *nigra.*
,, *nigrescens.*
Porphyra laciniata.
Ptilota plumosa.
Rhodomela subfusca.
Rhodymenia palmata.
Sphacelaria cirrhosa.
Ulva lactuca.
,, *latissima.*

This list, which is not in any sense complete, contains 55 spp. in 41 genera, all of which have been previously recorded for Fife.

Note on Reagents.—The specimens left by Terras were variously preserved in: Burchardt 50 per cent. + Sea Water 50 per cent; Gibson 50 per cent. + Sea Water 50 per cent.; Burchardt-pure; Formaldehyde 50 per cent. + Sea Water 50 per cent.; and, of these, the last mixture was the only one satisfactory throughout.

Micro-preparations of the species recorded above are preserved in the Department of Botany, St. Andrews.

I am indebted to the Carnegie Trust for a research grant, to the University of St. Andrews for laboratory facilities, and to Professor R. J. D. Graham for supervision and encouragement.

Summary.

1. There has been no published record of a survey of the algae of the Fife coast for the past forty-six years, and former surveys have been confined to Elie.

2. The present survey, initiated by the late Mr. J. A. Terras, was intended as an extension of previous surveys.

3. 107 spp. in 71 genera are recorded for the coast from Crail to Fife Ness.

4. Ten species have been added to the algal flora so far recorded for the coast of Fife.

5. Certain peculiarities concerning the times of fruiting of several species are noted.

6. A general survey of the algae of St. Andrews Bay is attempted, 55 spp. in 41 genera being noted.

7. Formaldehyde 50 per cent. + Sea Water 50 per cent. is noted as the best of several preservatives.

References.

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(2) Traill, G. W.: Monograph of Algae of Firth of Forth (1855).
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(4) Newton, L.: A Handbook of British Seaweeds. B.M. (1931).

Notes on Lichens, mainly from Orkney, in the Herbarium of the Royal Botanic Garden, Edinburgh.

By Walter Watson, D.Sc., A.L.S.

(Read 13th June 1935.)

During recent years I have examined a large number of lichens from the herbarium of the Royal Botanic Garden, Edinburgh. The story of the inception and results of this work is of some interest as it indicates some of the advances which have been made in the study of lichens. When most of the lichens in the herbarium were collected and named the taxonomic position of these plants was very doubtful, their symbiotic nature had not been recognised, and the genera were far more comprehensive than they are to-day. For many years I have considered that a methodical analysis of the distribution of these plants in the British Isles was desirable, and that such knowledge would be of material assistance in regard to the origin and relationships of the British flora. The works of British lichenologists were consulted, lists from Victoria County Histories and from many Floras were obtained, and as much assistance as possible was got from contemporary lichenologists. Eventually my material was sufficient to justify the formation of a preliminary Census Catalogue in which the lichens were listed and the botanical vice-counties in which they occurred, given. Mr. William Young knew of this work and kindly offered to assist me by looking through the Edinburgh herbarium. It was with great pleasure that I sent him a duplicate typescript copy of my attempts at making a Census Catalogue. In a painstaking and most praiseworthy way he compared the lichens in the herbarium with my list and was able to add over 1000 vice-county records. This work was all the more difficult as the naming and arrangement of the lichens in my list often differed widely from those adopted in the herbarium. Many of these lichens were under old names, or under names which had been used in various ways by the older lichenologists, so that it was considered advisable to examine some of the plants

on which the records were based. Some unnamed plants collected by Lindsay from the Orkneys (v.c. 111) in 1866 were also examined.

Definite determination was impossible in some cases, but the general examination yielded some interesting results. A new species, *Lecidea atroides*, is described further on, whilst *L. brachyspora* and *Acarospora atrata* are new to the British Isles. Some of the plants which Lindsay collected were undescribed at the time. *Aspicilia complanatoides* was not described till 1918; *Lecidea scutellata* till 1932; and *L. kittilensis* till 1934.

In the following list an asterisk denotes a new vice-county record. S. and Sm. are used as contractions for Stronsay and Stromness respectively. The arrangement follows on the lines of that advocated by me in "The Classification of Lichens," *New Phytologist* (1929).

List of Lichens.

Usnea protensa Stirt., Scot. Nat. vii (1883–84), 76. The specimen from Garrock Wood (73) on which the species was published was found in herb. McAndrew. Stirton's description is a short one. "*Usnea protensa* sp. nov.—Similis *U. subsordidae* (Strn.) sed robustior et pendule, longitudine (·5–1)-pedalis. Prope New Galloway Scotiae a cl. J. McAndrew lecta." The reference to *U. subsordida* Stirt. (Scot. Nat., vi, 1881–82) indicates that the reaction of the medullary fibrils is K yellowish then reddish, I–, and that it has some appearance of *U. ceratina*. The thallus is pendulous, 6–12 inches long, rigid, often darker than *U. ceratina* and sometimes approaching in colour to *U. sublurida*. The reaction of the medullary fibrils to potassium hydrate is very distinctive. At first they become yellow, then deep orange yellow, and finally red. The chondroid axis is usually pale but in older portions becomes darker. The position of Stirton's species of *Usnea* is not satisfactory. *U. subpectinata*, *U. hirsutula*, *U. intexta*, *U. rubicunda*, *U. sublurida*, and *U. constrictula* are some of the British species which have never found places in an authoritative work on British lichens except as forms of other species. Some of the names have recently been adopted by Motyka in his

revision of the genus. A Somerset specimen which has been determined by Motyka as *U. sublurida* is very similar to the Garrock Wood specimen even in regard to the supplementary reddish coloration of the medullary fibrils on treatment with potassium hydrate. *U. sublurida* Stirt., however, is in the section where the medullary fibrils merely become yellow with potassium hydrate. Personally I am inclined to regard some of the so-called species as varieties or merely forms.

Parmelia saxatilis var. *laevis* Nyl. Dailly (75*) A. Gray.

P. omphalodes var. *panniformis* Ach. Sm. (111*).

Platysma sepincolum Hoff. The specimens from Penzance (1) *leg.* Curnow and Waterfall, and from Stokesley (62, *leg.* Mudd) belong to *P. chlorophyllum* (Humb.) Wats.

Squmaria radiosa (Hoff.) Poetsch. A specimen from Keighley referred by Hebden to this under the synonym *S. circinata* is *S. muralis* (Schreb.) Elenk.

Lecanora albescens (Hoff.) Flk. (*L. galactina* Ach.). S. (111*).

L. campestris (Schaer.) Hue. S. (111*); Scrabster (109*).

L. atra Ach. S. and Sm. (111).

L. umbrina Mass. Scrabster (109*); S. and Sm. (111*); form *gregata* Harm., Scrabster (109*).

L. hageni Ach. form *roscida* (Somm.). S. (111*).

L. sulphurea Ach. Sm. (111).

L. polytropa Schaer. S., Sm., and Hill of Hoy (111).

L. intricata Ach. A plant from Whernside under the name of *Acaraspora smaragdula* is *L. intricata* as suggested by Hebden on the packet.

L. epanora Ach. Hill of Hoy (111*).

L. badia Ach. Sm. (111*).

L. cenisia var. *atrynea* (Ach.) Harm. Scrabster (109*).

L. sordida Th. Fr. *L. rupicola* Zahl. A specimen collected by McAndrew at Ravelston (83) and questioned by Hebden is correct. The spores are within the size limits of *sordida*.

L. fugiens var. *chlorophaeoides* (Nyl.) A. L. Sm. A specimen collected by Lindsay at Stronsay in 1866 is near to this, but the thallus is much more definite than in any British specimens which I have seen.

Thallus tawny-yellowish, cracked areolate, determinate and limited by a dark hypothallus, K faint yellowish, C

orange yellow to orange reddish, KC orange red, I–. Apothecia pale brown, reddish-brown to dark brown, subinnate to appressed becoming more prominent, concave to plane or convex, with thalline margin, epruinose, 0·2–0·4 mm., little affected by K or C. Paraphyses discrete, brownish or pale dirty violet at clavate apices. Hypothecium colourless with green algae below. Hym. gel. blue then greenish-indigo with iodine. Spores 8 simple, colourless, with a well-defined wall but no epispore, 11–12 by 5–5·5 μ, apparently mature though asci are few and often ill-developed.

Ochrolechia parella f. *crenularia* (Cromb.) Zahl. S. (111).

Aspicilia cinerea (Ach.) Krb. Newburgh (85*).

A. complanatoides (A. L. Sm.) comb. nov.; *Lecanora complanatoides* A. L. Sm., Mon. Brit. Lich., part i. (1918), 326. Stronsay (111*).

Biatora fuscorubens Nyl. On calcareous rocks, Sm. (111*).

B. phaeops (Nyl.) Arn. A plant from Stromness probably belongs here, but as only spermogonia are present the determination is uncertain.

Lecidea latypea Ach. S. and Sm. (111*).

L. goniophila (Flk.) Schaer. On arenaceous rocks, Scrabster (109*); S. (111*).

L. subsequens Nyl. On calcareous rocks, Scrabster (109*).

L. lapicida Ach. Don's specimen from near Forfar (90) is probably correct though no well-developed spores are present. Lindsay's specimen from the foot of Ben Lomond (86) is without spores but seems more like *L. plana*. Lindsay's specimen from Blackcairn Hill, Newburgh (85), has no relationship to *lapicida* but is a member of the *contigua* group and is better placed under *L. percontigua*.

L. leucophaea (Flk.) Nyl. Scrabster (109*).

L. lithophila Ach. Hill of Hoy (111*).

L. subkochiana Cromb. Scrabster (109*).

L. plana Nyl. See *L. lapicida*.

L. rivulosa Ach. Hill of Hoy and Stromness (111*) with form *depressa* Leight. (which is the form often taken as the type), and form *cyathoides* Ach.

L. tenebrica Nyl. Garrynahine (110*). Apothecia not well-developed but it seems nearest to this species.

L. contigua (Hoff.) Th. Fr. Scrabster (109*), S. and Sm. and Hoy (111). A form with composite apothecia came from the Hill of Hoy. It has some resemblance to *L. pycnocarpa* Krb., but the internal characters are different.

L. percontigua Nyl. Newburgh (85*); Sm. (111*).

L. scutellata Wats. Kirkwall and S. and Sm. (111*).

L. albocoerulescens (Wulf.) Ach. Scrabster (109*).

L. crustulata (Ach.) Krb. Kirkwall and S. and Sm.* (111); var. *meiospora* (Nyl.) Oliv. Kirkwall, Stromness, and Hill of Hoy (111*); Lerwick (112*).

L. deparcula Nyl. Hill of Hoy (111*).

L. auriculata Th. Fr. Kirkwall and Sm. (111*). The apothecial margin is usually less flexuose than usual. Specimens showing this character belong to the form *sarcogyniza* (*L. sarcogyniza* Nyl.). This form is more frequent than the type.

L. brachyspora Th. Fr. Kirkwall and Sm. (111*). This has not been previously reported from the British Isles. It is similar to *L. auriculata* except for the spores which are small and subglobose.

L. sylvicola Flot. Sm. (111*).

L. soredizodes (Lamy.) Lindau. Stromness (111*).

L. atroides Wats., J. of Bot. (1935), 151. Thallus effuse, cracked areolate or of dispersed areolae, ochraceous, orange yellow with potassium hydrate, with green algal cells about 10 μ diam. Apothecia small, black, $\pm$ shining, lecideoid, at first innate in the areolae, later convex and immarginate with dark epithecium, violet or dark violet hymenium, clavate asci and pale or colourless hypothecium. Paraphyses coherent, thickish, septate, apparently swollen above. Spores simple, colourless, 8–nae, $11 \times 6\ \mu$, with distinct wall, often appearing uniseriate and globose, $8 \times 7\ \mu$. Hymenial gelatine blue then sordid with iodine. On siliceous rock, Hill of Hoy, Orkney (111*), *leg.* Lindsay, 1866.

The intense violet coloration of the hymenium is so reminiscent of that shown in *Lecanora atra* that it might almost pass for a lecideoid form of that species were it not for the ochraceous thallus with its slightly reddish reaction with potassium hydrate. The plant has a general external resemblance to *Lecidea fuscoatra* Ach.,

but there is no reaction to calcium hypochlorite and the internal characters are different.

"*L. tessellata* Flk." A plant collected on siliceous rock by Lindsay in 1866 from Scrabster (109) has some kinship with this species but the thallus is more verrucose and the spores are smaller. It is described below. Thallus verrucose-granulate, ± cracked areolate, verrucae about 0·3 mm., areolae often larger, grey, whitish-grey, or pale yellowish-grey, doubtfully determinate or subdeterminate, with almost a negative reaction to potassium hydrate (faint yellowish becoming very slightly reddish when dry), KC–, C–, medulla with a distinct bluish coloration with iodine in places (and shown under microscope) but not continuously coloured; a dark hypothallus is not very evident though a dark line (? alien) is sometimes present at the margin of the thallus; algal cells green, about 12 μ diam. Apothecia dark, lecideoid, with dark proper and prominent margin (sometimes shining); no algal cells beneath the hypothecium; disc dark with a very faint reddish tinge. Epithecium dark, thickish, about 25 μ. Hymenium about 60 μ, blue then sordid with iodine, without violet granules but with pale bluish-violet tinge (sometimes very slight), accentuated by K and reddish-violet after HNO_3. Paraphyses septate, ± loosely coherent or subcoherent (discrete after K or HNO_3) with confluent dark brown or dark bluish swollen apices (dark purplish after K and reddish after HNO_3). Asci small, clavate (sometimes swollen), or somewhat cylindrical. Hypothecium pale brown of ± erect hyphae, but variable in arrangement. Spores colourless, simple, small, 5–7 × 3–5 μ (perhaps ill-developed), sometimes globose or subglobose. *L. serenior* Vain. Lich. Fenn. iv, 250 (1934) and *L. kittilensis* Vain., *ibid.*, 135, both of which, according to description, have a definite dark hypothallus, have many characters agreeing with the Scrabster lichen. If one considers that the spores are mature, then it agrees better with *L. kittilensis*, which has the thallus greyish or whitish, areolate, esorediate, K–, C–, KC–, I bluish for medulla, hypothallus dark. Apothecia 0·3–1 mm., usually at first ± innate but at length adnate, epruinose, plane, black, slightly

shining with thinnish but prominent and persistent proper margin. Hypothecium fuscous; epithecium dark brown. Paraphyses coherent. Asci broadly clavate. Spores 8–nae, subglobose or ellipsoid 4·5–7 × 3–5 μ. In *L. serenior* the thallus is moderately thick, verrucose or verrucose-areolate, esorediate, K–, C–, KC–, I bluish for medulla, greyish with dark hypothallus. Apothecia at first immersed, then emergent and lecideine, dull black, epruinose, with dark entire thin but lightly prominent margin. Hypothecium pale. Epithecium violaceo-fuligineous, becoming bluish with K; paraphyses loosely coherent; asci cylindric or cylindrico-clavate. Spores 8–nae, ellipsoid or subglobose, 7–12 × 5–8 μ.

"*L. neglecta* Nyl." A plant collected by McAndrew from Trochie Braes, New Galloway (73), in 1891 had some resemblance to this species and was given a new name expressing that resemblance by Nylander. The name appears to be unpublished and is unnecessary. An examination of the apothecia convinced me that they belonged to "*L. neglecta*" but were on two different thalli, one of which was *Diploschistes scruposus* var. *bryophilus* and the other similar to *Stereocaulon condensatum*. On the former the apothecia did not seem to develop properly but on the latter normal development occurred. The apothecia of "*L. neglecta*" apparently belong to a parasitic fungus and its proper host is that on which normal development occurred. This view as to the parasitic nature of the apothecia has been adopted by a number of lichenologists. The parasite is known as *Nesolechia neglecta* Vain. The sterile thallus on which the parasite usually grows has been described as *Crocynia neglecta* Hue, but the thalli of the proper host in the New Galloway combination or in that from Ben Lawers (according to description) do not appear to belong to *Crocynia*.

Pertusaria leioplaca v. *hymenina* Ach. Suffolk "from Mr. Turner" in Menzies' herbarium. This is *P. Wulfenii* DC. for which the above name is an almost forgotten synonym.

P. concreta Nyl. Garrynahine (110*); form *Westringii* (Ach.) Nyl. (=*P. pseudocorallina* Arn.). Fort William (97*) under the name of *P. communis*.

P. sulphurea f. *variolosa* Schaer. Hill of Hoy (111*).

Acarospora smaragdula (Wahl.) Krb. Stronsay (111*). As this specific name had often been misused by British lichenologists it was considered advisable to examine other specimens so named. The specimen from Whernside (64), Hebden considered to be *Lecanora intricata* and was quite correct in doing so. Those from Braid Hills and Salisbury Crags (83) and Lomond Hills (85) are *A. fuscata*. That from Bracklinn Bridge, Callander (87), is a puzzling plant but seems to belong to the group of *A. discreta* but is not *A. veronensis* Mass., the species to which Magnusson has referred all the British members of that group. That collected from Cork Harbour (I. 4) by Carroll is correct.

A. fuscata (Schrad.) Th. Fr. *See* above and below.

A. peliscyphoides (Nyl.) Oliv. Magnusson in his Monograph of *Acarospora* discards this name and it was therefore considered advisable to examine the two specimens so named in the herbarium. That from Braid Hills (83) was examined by Hebden who correctly named it *A. fuscata*. That from Balerno (83) also seems better placed as *A. fuscata*. I see no reason to adopt the name *peliscyphoides* for a variety of *A. fuscata*.

A. discreta Nyl. *See* under *A. smaragdula*. Some of the segregates of this species seem scarcely worth distinguishing except as forms.

A. atrata Hue. On arenaceous rock, Stromness (111*), *leg.* Lindsay, 1866. New to the British Isles. Thallus indeterminate separated by deep cracks into small brown to dark reddish-brown areolae, K–, C–, margin dark but pale beneath where attached to stone. Apothecia 2–6 in each areolae, immersed, concolorous with the thallus or darker, immersed, usually with a distinct thalline margin. Epithecium darkish brown. Hymenium under 90 μ, wine red with iodine. Paraphyses $\pm$ discrete, apparently slightly beaded. Hypothecium colourless, bluish-green with iodine. Spores numerous and minute.

Ramalina siliquosa (Huds.) A. L. Sm. The specimen said to have been collected by J. Brodie in Staffordshire seems to be correct for *R. cuspidata*. The lichen is a maritime one and its collection in an inland county is a peculiar

circumstance. The specimen from N. Berwick Law (82) agrees with *R. cuspidata*. That from Burntisland (85) is *R. cuspidata* with some form *rugosa* Oliv. Lindsay's plant from N. Berwick Law (82) is *R. scopulorum* and very near var. *incrassata* Nyl. Those from near Talisker, Skye (104), and McAndrew's specimen from Tarbert, L. Fyne (101), are better under *R. Curnowii*.

R. scopulorum (Retz.) Ach. and var. *incrassata* Nyl. *See* above.

R. Curnowii Cromb. *See* above.

R. cuspidata Nyl. and form *rugosa* Oliv. *See* above.

R. subfarinacea Nyl. Hebden's specimen from Clapham (64) is correctly named even though the district is an inland one.

R. farinacea Ach., Dailly (75); form *minutula* Ach. Watten (109), Lillie.

Lecania prosechoides (Nyl.) Oliv. Stronsay (111*).

L. erysibe Mudd. Hill of Hoy (111*); var. *sincerior* (Nyl.) B. de Lesd. S. (111*).

L. Hutchinsia (Nyl.) A. L. Sm. S. (111*).

Biatorina biformigera (Leight.) A. L. Sm. Hill of Hoy and Stronsay (111*).

B. nigroclavata (Nyl.) Arn. *Lecidea nigroclavata* Nyl. On alder, near Darsallock, New Galloway (73), *leg.* J. McAndrew, 1889. This was given a new specific name by Nylander but it was never published. McAndrew's pencil note of "*lenticularis*" suggests its true affinity. *B. lenticularis* and *B. nigroclavata* are very similar except that the latter is corticicolous and has spores less constantly one-septate.

Catillaria chalybeia (Borr.) Mass. Scrabster (109*); Sm. (111*).

Toninia squamulosa (Deak.) Mudd. Scrabster (109*); S. (111*).

Toninia syncomista (Flk.) Th. Fr. Scrabster (109*); S. (111*). There is some doubt as to the specific name of this plant. In A. L. Sm. Mon. (1926) it is given as *leucophaea*, but *sabulosa* and *lobulata* also have some claims for priority.

Bilimbia sabuletorum Arn. and var. *obscurata* A. L. Sm. S. (111*).

Bacidia umbrina (Ach.) B. and R. Sm. (111*).

Haematomma ventosum Krb. A plant named "*L. rupestris*" in Menzies' herbarium was this. *L. rupestre* is usually considered to be a synonym of *Callopisma* (*Placodium*) *rupestre.*

Xanthoria parietina (L.) Th. Fr. Scrabster (109*); S. (111*).

Placodium callopisma var. *plicatum* (Wedd.) Leight. S. (111*).

P. lobulatum (Flk.) Flag. S. (111*).

P. erythrocarpum (Pers.) Anzi. S. (111*).

P. elegans DC. There were several plants under this name. That from Ken Bridge, New Galloway (73), *teste* Nyl. is perhaps better placed with *elegans.* Those from School walls, New Galloway (73), and from near Edinburgh (83) (*leg.* Maingay) are certainly *P. dissidens.*

P. dissidens Nyl. *See* above.

Callopisma aurantiacum var. *flavovirescens* (Wulf.) Krb. S. (111*).

C. pyraceum (Ach.) Arn. and var. *holocarpum* (Ehrh.) Stein. Scrabster (109*) and S. (111*).

C. ferrugineum var. *festivum* Mudd. S. (111).

C. fuscoatrum (Bayrh.) comb. nov.; *Placodium fuscoatrum* A. L. Sm., Mon. Brit. Lich., part i (1918), 219. S. (111*).

C. caesiorufum (Ach.) Wats. Scrabster (109*).

C. ochraceum (Schaer.) Mass. S. (111*).

C. vitellinulum (Nyl.) Arn. S. (111*).

C. epixanthum (Ach.) Mudd. Scrabster (109*).

Candelariella vitellina (Ehrh.) Mull. Sm. (111*).

Physcia hispida (Schreb.) Tuck. (*P. leptalea* DC.) Coolins (104), Gilchrist in part; Watten (Lillie) and Scrabster (109); Carrigaloe (I. 4) Carroll; Bunbeg (I. 35) Dickie; var. *tenella* (Scop.) Wats., Peckford (34) Reader; Wigton (74) McAndrew; Dailly (75) A. Gray; Innerleithen (78) Lindsay; Brodie House (97) Dickson; Coolins (104) Gilchrist.

P. grisea (Lam.) Zahl. In Menzies' herbarium as *Parmelia farrea* Ach. (a synonym).

P. stellaris (L.) Nyl. As this name has been so often applied in a broader way than it is to-day it was considered advisable to examine all the specimens so named. Those from Buckland Farringdon (22) Milne; Woodchester (34)

Reader; Dumfries (72) Lindsay; Glen Nevis (97) Lindsay; Ethie (90) W. Smith and Reader; Kyles of Bute (100) Lindsay; and Tarbert (101) McAndrew, are *P. aipolia* var. *cercidia*. Those from Invermoidart (97) Macvicar; and Lochgilphead (98) McAndrew are *P. aipolia*. Carroll's plant from Carrigaloe (I. 4) is given in Knowles' Lich. Ireland as *P. stellaris*. It seems to be a mixture of *P. stellaris* f. *granulata* B. de Lesd. and *P. hispida*. McAndrew's specimen from New Galloway (73) is *P. stellaris* f. *rosulata* (Ach.) Nyl.

P. aipolia (Ach.) Nyl., and var. *cercidia* Th. Fr. *See* above.

Rinodina demissa (Krb.) Arn. S. (111*).

Buellia myriocarpa (DC.) Mudd. S. (111*).

B. aethalea (Ach.) Th. Fr. Sm. (111*).

B. advenula (Leight.) A. L. Sm. *Karschia advenula* Zopf. Garrynahine (110*) *leg.* Lindsay. This corresponds with the description in the Mon. Brit. Lich. 200 (1926) except that the number of spores in the ascus were eight instead of four. Leighton described the plant in Trans. Linn. Soc. Bot. (1876) as having eight spores, and in his type specimen there are eight.

Rhizocarpon alboatrum var. *epipolium* (Ach.) A. L. Sm. Scrabster (109*) Stronsay (111*): form *microcarpum* B. de Lesd., Stronsay, differs chiefly from the usual form in the smaller apothecia (under 0·4 mm). The thallus in the Stronsay plant is more definite than described by Lesdain.

R. geographicum DC. Garrynahine (110); S., etc. (111*).

R. petraeum (Wulf.) Mass. and var. *excentricum* A. L. Sm. Scrabster (109*).

R. confervoides DC. Stromness (with f. *fuscescens* A. L. Sm.) and S. (111).

Diploschistes scruposus var. *bryophilus* Mull. New Galloway (73*) McAndrew.

D. ocellatus (DC.) Norm. is the plant mounted in Menzies' herbarium as *Lecanora Villarsii* Ach. No locality is given but the plant is not British.

Cladonia leptophylla Flk. Three specimens so named were in the herbarium. Mudd's specimen from Easby (62) is *C. parasitica*, and a similar specimen from him and from the same locality is so named in the Brit. Mus.

McAndrew's and Hebden's specimen from Tarbert (101) is *C. pityrea* form *crassiuscula*. McAndrew's plant from near Portpatrick (74) appears to be correct.

C. pityrea Fr. form *crassiuscula* Wain. Tarbert (101). *See* above.

C. cervicornis Schaer. Harden Moor (63) Hebden, Ingleboro' (64), Carrington. That from Holyhead mountain (52) is var. *subcervicornis* (Wain.) and one piece is almost *C. verticillata* Flk.

C. cornuta (L.) Fr. McAndrew's specimen from New Galloway (73) seems more like *C. ochrochlora*. A specimen from him and from the same locality is so named in the Brit. Mus.

C. ochrochlora Flk. *See* above.

C. symphicarpia Arn. The specimen from Bramble Hill (11, *leg.* Livens) in McAndrew's herbarium was so named by Hebden. It is *C. caespiticia* Flk. and not any of the *symphicarpia* group.

C. hypophylla from Helvellyn (*leg.* J. A. Martindale) is *C. lepidota* form *hypophylla* (Nyl.) Cromb. of Mon. Brit. Lich. 148 (1894). Nylander placed it as a form of *C. degenerans* Spreng.

C. turgida Hoff. As in so many other cases of plants so named McAndrew's specimen from Castle Douglas (73) is wrong. It is *C. uncialis* form *turgescens* Del. A similar specimen from the same collector and from the same locality is so placed in the Brit. Mus.

"*C. extensa*." On the ground, Charlton (85) refers to *C. coccifera* form *extensa* Flk.

C. cyathomorpha Wats., J. of Bot. (1935), 156. Squamules large, 5–10 mm. broad, sometimes flat but often incurved convoluted and ± erect (cyathomorph), pale tawny-yellowish above, K– or faint yellowish, C–, white below, K– C–, with folds ± similar to the bands or veins in Peltigera but less definite and becoming slightly reddish with K. Podetia on surface of squamules, 4–10 mm. by 1–1·5 mm., sometimes ± pitted, often slightly squamulose or irregularly verrucose, expanding to form a scyphus ± granulate within and with small or minute brown apothecia on the margin. Spores not seen. Collected by McAndrew from near Loch Dungeon, New Galloway

(73), in 1881, and considered to be a new species by Stirton though apparently never published. It is near to *C. foliacea* Willd., but distinct in the veining beneath and in the cup-like shape which the ± erect and convoluted squamules often assume. It is associated with *Rhacomitrium heterostichum* so that its habitat was presumably mossy rocks.

Pycnothelia papillaria Duf. Stornoway (110*).

Stereocaulon denudatum Flk. New Galloway (73) McAndrew.

S. condensatum Hoff. See *Lecidia neglecta*, p. 511.

Crocynia lanuginosum (Ach.). Hue Brown's "*Byssus bicolor*" from the North of Ireland belongs here. A mounted specimen in Menzies' herbarium labelled *B. phosphorea* is a fungus (*Corticium* sp.).

Peltigera spuria var. *erumpens* Th. Fr. Harden Moor (63). This is like the specimen from the same locality sent by Hebden to me. I consider it to be a small form of *P. rufescens* var. *praetextata* Nyl.

Nephromium resupinatum (L.) Fr. A number of plants so named were in the herbarium. They were all examined as the name has so frequently been misapplied, and it is of interest to know what are the actual species to which the name was given. Those from Baysdale (62) Mudd; Ingleboro' (64) Carrington; Keswick (70) Leighton; Minto Crags (80) Maingay; near Callander (87) Lindsay; Loch Awe and Crinan Canal (98) Barclay are *N. lusitanicum*. That collected by A. C. Maingay in 1855 from shady rocks at Aberfeldy (88) is the rare *N. laevigatum*.

N. tomentosum from Pass of Leny (87) is *N. lusitanicum*.

N. laevigatum (Ach.) Nyl. As stated above Maingay's specimen of *N. resupinatum* from Aberfeldy (88) belongs here. The specimens from Penzance (1) Curnow, Baysdale (62) Mudd, Falls of Foyers (96) Lindsay, are *N. lusitanicum*. Waterfall's specimen from v.c. 3 is *N. lusitanicum* var. *hibernicum*. The specimen from Tarbert (101) McAndrew, is *N. laevigatum* var. *parile* (Ach.) Nyl.

N. lusitanicum (Schaer.) Nyl. *See* above. Var. *hibernicum* Nyl. *See* above.

Parmeliella perfurfurea (Nyl.) Zahl. Burnfoot Hill, New Galloway (73), J. McAndrew. This species has escaped the notice of our lichenological authors. It was published

by Nylander in Acta Soc. Fenn., xxvi (1900), No. 10, p. 29, footnote, as follows:—

"*Pannularia perfurfurea* Nyl., cui thallus fuscus tenuiter furfurascus effusus; apothecia fusca plana mediocria (latit. 0·5 millim.) margine non prominulo subpallescente; sporae breviter ellipsoideae, long. 0·009–0·010, crass. 0·005 mm., I gel. hym. fulvescens. Muscicola in Scotia, New Galloway (James McAndrew)." Thallus furfuraceous, non-gelatinous, effuse, of minute brown squamules. Apothecia about 0·5 mm., brown, plane, sometimes ± concave or ± convex, with a paler proper margin, entire but sometimes slightly flexuose. Hypothecium colourless but merging into brownish epithecium above and into brownish hypothecium below, about 50 μ. Epithecium brownish with many dispersed granules. Ascus clavate but sometimes more cylindrical, about 35×13 μ. Spores eight in ascus, irregularly arranged (sometimes horizontally parallel in ascus), colourless, simple, $9–10 \times 4·5–5$ μ. McAndrew found the plant on Burnfoot Hill (73). It seems quite distinct from any other Parmeliella.

Leptogium crenulatum Wats., J. of Bot. (1935), 158. Laciniae narrow, crenulate, brownish to dark when dry, gelatinous and olivaceous-black when moist, usually ± flattened, often concavo-convex in section (with negative reaction to iodine), about 160 μ thick, closely intricate in various directions. Medullary hyphae fairly lax, cortex more compact and yellower with a slight indication of cellular structure (pseudoparenchyma). Algal cells (Nostoc) in undulating chains of 4–15. Apothecia absent. In McAndrew's herbarium as a new species of "Collemodium" according to Nylander, but apparently never published. Collected from Ben Lawers (88) by McAndrew in 1885. A pencil note on the packet suggests its affinity with *L. Schraderi* Nyl. It differs from *L. Schraderi* in the less cylindrical (often concavo-convex in section) and more crenulate laciniae which are arranged in a less erect and more intricate manner and are less wrinkled when dry, in the less definite pseudoparenchymatous cortex (both in section and in surface view) and in the negative reaction with iodine.

"*Collema glomerulosum*." Penzance (1, Curnow) and Killarney (Carroll). This is *Myriangium Duriaei* M. & B., a fungus which has an external resemblance to a Collema and was formerly included in that genus under the above name.

Collema elveloideum Ach. from Iver near Uxbridge (24) appears to be *C. tenax* v. *palmatum* Harm. *Lempholemma elveloideum* (Ach.) Zahl. has not been found in the British Isles.

Lemphollema polyanthes (Ber.). Keighley (63, T. Hebden). This is sometimes given under the name of *L. myriococcum* (Ach.) Krb.

Spilonema scoticum Nyl. Bennan Hill, New Galloway (73). McAndrew's specimen of *Stigonema pulvinatum* (Breb.) had fungal threads with the alga but no apothecia were seen.

Arthonia ilicina Tayl. On holly, Moidart (97*) Macvicar.

Opegrapha calcarea Turn. var. *heteromorpha* (Stiz.) nov. comb.; *O. calcarea* form *heteromorpha* A. L. Sm., Mon. Brit. Lich., 237 (1911). On siliceous rock, Scrabster (109*).

O. confluens Stiz. S. and Sm. (111*).

"*O. epiphega*," *Lichen vugasus* E. Bot. On trees near the R. Noran (90) *leg.* Don, and given on Turner's authority. This is the fungus *Dichaena faginae* Fr. for which the above are old names, as it was confused with lichens.

O. herpetica Ach. var. *elegans* Borr., Woodchester (34*), Reader.

Chiodecton myrticola Fee. Moore's specimen from Antrim (I. 39) is not this but *C. albidum* (Tayl.) Leight. It is recorded as *C. albidum* in Knowles' Lich. Ireland.

Phaeographis dendritica (Ach.) Mull. from Birkhill Woods, *leg.* Fulton, is *Graphina anguina* (Mont.) Mull, which is new to v.c. 85.

P. Lyellii (Sm.) Zahl. from v.c. 90, *leg.* Don, is correct and new to the county.

Dermatocarpon cinereum (Pers.) Th. Fr. Kirkwall (111).

Verrucaria maura Wahl. Scrabster (109*); S. (111).

V. pseudomemnonia Zsch. Scrabster (109*). This is the plant to which the name of *V. maura* var. *memnonia* was formerly applied.

V. microspora Nyl. S. (111*).

V. microsporoides Nyl. Scrabster (109*).

V. macrostoma DC. Bracklinn Bridge, Callander (87*). On the same stone as the Acarospora collected by Lindsay.

V. hydrela Ach. Carroll's specimen from near Cork (I. 4) is *V. laevata* Ach. Apparently this correction had previously been made as *V. hydrela* is not in Knowles' Lich. Ireland for Co. Cork. Some *V. aethiobola* Wahl. and *V. papillosa* Ach. are on the same stone as *V. laevata*. The three last-mentioned are given in Knowles' Lich. Ireland for I. 4.

V. myriocarpa Hepp. Walls about Cork (I. 4), Carroll. In Knowles' Lich. Ireland, this locality is given for *V. murina* Leight. The two names are synonymous but *V. murina* Leight. is not the same plant as *V. murina* Ach., therefore Leighton's name should be discarded. Carroll's specimen, when examined, was found to be *V. muralis* v. *submuralis* Oliv.

V. mutabilis Borr. Scrabster (109*); S. (111*).

V. prominula Nyl. Stornoway (110*).

V. muralis Ach. Scrabster (109*), S. and Sm. (111*); var. *submuralis* (Nyl.) Oliv. Walls about Cork (I. 4), Carroll as *V. myriocarpa*.

V. rupestris Schrad., var. *ruderum* Nyl. Scrabster (109*).

Dacampia Hookeri (Borr.) Mass. Ben Lawers (88). This is the plant given on a mounted sheet in Menzies' herbarium under the name of *Lecidea nigropunctata* Hook. Fl. Scot., ed. 2.

Polyblastia deminuta Arn. Sm. (111*).

Arthopyrenia stigmatella (Sm.) A. L. Sm. This is the lichen from v.c. 90 to which Don gave the name of *Verrucaria cinerella* Flot. It is not *Microthelia micula* Flot. to which plants named *V. cinerella* usually belong.

A. leptotera (Nyl.) A. L. Sm. The plant collected from Tenby (45) by E. M. Holmes seems more like *A. marina* though no spores showing three definite septa were seen. The spore size was that of *A. marina* A. L. Sm., with which I should place it.

Stigonema pulvinatum (Breb.). See *Spilonema scoticum*.

Myriangium Duriaei M. & B. See *Collema glomerulosum*.

Phaeospora rimosicola (Leight.) Zopf. A fungus parasitic on the thallus of *Rhizocarpon petraeum*. Scrabster (109).

Discothecium gemmiferum (Tayl.) Vouaux. A fungus parasite on Pertusaria, Garrynahine (110).

Report of the Annual Conference of the Cryptogamic Society of Scotland, 1935.

By Rupert Smith.

(Read 17th October 1935.)

The Fifty-fourth Annual Conference of the Cryptogamic Society was held at Dumfries on 24th, 25th, and 26th September 1935, with headquarters at King's Arms Hotel.

The foray on Tuesday 24th was in the woods at Capenoch, Penpont, the property of H. S. Gladstone, Esq. Although the weather was dull and showery a good collection of species was noted.

On Wednesday 25th the rendezvous was at Castlemilk, near Lockerbie, belonging to Sir John Buchanan-Jardine.

An enjoyable day was spent in the extensive woods, and although fungi were plentiful the variety of species was not so great as one would have expected.

The third foray, as arranged, had to be abandoned on account of the weather being cold and very wet. Among the fungi collected may be mentioned *Amanita phalloides*, one of the most poisonous known, and *Cordyceps militaris*, an interesting species parasitic on caterpillars.

At the evening meeting on Wednesday 25th, Mr. R. H. Johnstone occupying the chair, a resolution was recorded in the minute book expressing the Society's great loss by the death of its Hon. Treasurer Mr. R. B. Johnstone and the Rev. Wm. M. Steven, both devoted and valuable members.

Mr. Rupert Smith was re-elected Hon. Secretary and thanked for the arrangements for the Dumfries Conference.

Callander was provisionally chosen for the 1936 Conference.

[List of Species.

LIST OF SPECIES GATHERED DURING THE FORAY.

Localities.

1. Capenoch, 24th September.
2. Castlemilk, 25th September.

Hymenomycetes.

Amanita muscaria (Linn.) Fr., 1, 2; pantherina (DC.) Fr., 1; spissa Fr., 1; mappa (Batsch) Fr., 1; rubescens (Pers.) Fr., 2; phalloides (Vaill.) Fr., 1.

Lepiota amianthina (Scop.) Fr., 1; procera (Scop.) Fr., 1.

Armillaria mellea (Vahl) Fr., 1, 2; mucida (Schrad.) Fr., 2.

Tricholoma albobrunneum (Pers.) Fr., 1; fulvum (DC.) Fr., 1.

Clitocybe suaveolens (Schum.) Fr., 1.

Laccaria laccata (Scop.) B. et Br., 1, 2; var. amethystina (Vaill.) B. et Br., 1, 2.

Collybia radicata (Relh.) Berk., 2; butyracea (Bull.) Fr., 1; velutipes (Curt.) Fr., 2; tuberosa (Bull.) Fr., 2.

Mycena pullata Berk. et Cke., 1, 2; cinerella Karst., 1; galericulata (Scop.) Fr., 1; filopes (Bull.) Fr., 2; galopus (Pers.) Fr., 2.

Omphalia fibula (Bull.) Fr., 1, 2.

Clitopilus prunulus (Scop.) Fr., 1.

Entoloma jubatum Fr., 1; rhodopolium Fr., 2.

Nolanea pascua (Pers.) Fr., 1, 2.

Leptonia lampropus Fr., 1.

Pholiota aurivella (Batsch) Fr., 2; spectabilis Fr., 2; mutabilis (Schaeff.) Fr., 2.

Inocybe rimosa (Bull.) Fr., 2; geophylla (Sow.) Fr., 2; hystrix Fr., 1.

Hebeloma crustuliniforme (Bull.) Fr., 1.

Flammula carbonaria Fr., 1; sapinea Fr., 2.

Galera tenera (Schaeff.) Fr., 1, 2; hypnorum (Schrank) Fr., 1, 2.

Psalliota campestris (Linn.) Fr., 2.

Stropharia semiglobata (Batsch) Fr., 1, 2.

Hypholoma fasciculare (Huds.) Fr., 1, 2.
Psilocybe semilanceata Fr., 1, 2; spadicea Fr., 1.
Panaeolus campanulatus (Linn.) Fr., 2.
Coprinus comatus (Fl. Dan.) Fr., 1; plicatilis (Curt.) Fr., 1.
Cortinarius (Inoloma) pholideus Fr., 1; (Dermocybe) cinnamomeus (Linn.) Fr., 2; (Telamonia) hemitrichus Fr., 2.
Paxillus involutus (Batsch) Fr., 1, 2.
Hygrophorus pratensis (Pers.) Fr., 1, 2; miniatus Fr., 1; chlorophanus Fr., 1; psittacinus (Schaeff.) Fr., 1, 2.
Lactarius turpis (Weinm.) Fr., 2; vellerius Fr., 1, 2; quietus Fr., 1, 2; vietus Fr., 1; rufus (Scop.) Fr., 1; cimicarius (Batsch) Cke., 1, 2.
Russula adusta (Pers.) Fr., 2; nigricans (Bull.) Fr., 2; rosacea (Pers.) Fr., 2; furcata (Pers.) Fr., 2; cyanoxantha (Schaeff.) Fr., 1, 2; fellea Fr., 1, 2; emetica (Schaeff.) Fr., 1, 2; fragilis (Pers.) Fr., 2; ochroleuca (Pers.) Fr., 1, 2; atropurpurea (Krombh.) Maire, 1, 2; Romellii Maire, 2.
Cantharellus cibarius Fr., 1.
Marasmius hariolorum (DC.) Quél., 2; ramealis (Bull.) Fr., 1.
Boletus badius Fr., 1; subtomentosus (Linn.) Fr., 2; chrysenteron (Bull.) Fr., 1; edulis (Bull.) Fr., 1, 2; luridus (Schaeff.) Fr., 1; scaber (Bull.) Fr., 2; duriusculus Schulz., 1.
Polyporus giganteus (Pers.) Fr., 1; betulinus (Bull.) Fr., 1, 2; lacteus Fr., 1, 2.
Polystictus versicolor (Linn.) Fr., 2.
Poria vulgaris Fr., 1; vaporaria (Pers.) Fr., 1, 2.
Irpex obliquus (Schrad.) Fr., 1.
Stereum spadiceum Fr., 1.
Corticium Sambuci (Pers.) Fr., 2; lividum (Pers.) Fr., 1.
Clavaria fusiformis (Sow.) Fr., 2; inaequalis (Müll.) Quél., 2; rugosa (Bull.) Fr., 1, 2.
Calocera viscosa (Pers.) Fr., 2; cornea (Batsch) Fr., 1.
Dacryomyces deliquescens (Bull.) Duby, 1.
Tremella mesenterica (Retz.) Fr., 1, 2.

Gasteromycetes.

Scleroderma aurantium Pers., 1, 2.
Lycoperdon echinatum Pers., 1; perlatum Pers., 2.

Pyrenomycetes.

Xylaria Hypoxylon (Linn.) Grev., 1, 2; polymorpha (Pers.) Grev., 2.
Cordyceps militaris (Linn.) Fr., 2.

Discomycetes.

Coprobia granulata (Bull.) Boud., 1, 2.
Calycella citrina (Hedw.) Quél., 2.
Coryne sarcoides (Jacq.) Tul., 2.
Rhytisma acerinum (Pers.) Fr., (as Melasma), 1, 2.

The Scottish Alpine Botanical Club Excursion, 1934.

By Robert Moyes Adam, F.L.S. (With Pls. XIV–XVI.)

(Read 17th October 1935.)

The annual excursion of the Club was carried through between 19th and 24th July, quarters being secured at High Force Hotel, 5 miles from the small town of Middleton-in-Teesdale, in County Durham.

Teesdale may be said to be unique of its kind, and is snugly tucked away in the heart of the Pennine Range. It lies in the "Fell" country, and is well populated even in the highest reaches. Small white-washed homesteads dot the landscape and give an air of well-being to the surroundings, especially beside High Force. The people subsist mainly by farming. This is of a pastoral character, and abundant proof was observed on all sides of the quality of the herds and the richness of the grazing. Grain and root crops are scarce in the higher parts of the valley, a fact explained by the climate and the lofty situation.

At one time Pyrites and lead ore were worked, and one relic of these industries did the Club a good turn. Leading up several of the hills were surprisingly good roads, which rendered transport an easy matter for the visit to Widdybank-fell.

As might be expected, it is largely to the geological character of the rocks that one must turn for an explanation of the nature of the flora seen. The formations of the underlying rocks belong to the Carboniferous series, sandstone, shales, and limestone being the principal rocks, the latter having an unexpected covering of deep peat. At other places where the limestone comes near the surface an increasing number of plants associated with limy soils occur. Volcanic rocks like Basalt and Dolorite appear in places, and both produce plant communities quite distinct from that of the limestone regions.

The drainage of the valley leads to the Tees, which at High Force is beautiful and charming, and also proved one of the most attractive hunting grounds, so that much time was

occupied in studying the plants and their environment near the stream.

Besides the Tees other watercourses were visited, and those also provided good ground, the Langdon Beck and the Harwood Beck being particularly rich spots. Some of the watercourses cut through peat and enter a calcareous boulder clay, and where this occurs some highly favourable soil results, over which flourish a large number of interesting species. It would seem that this same calcareous boulder clay underlies the meadows near Teesdale, for there is a particular luxuriance and variety there, among which many species are peculiar to Teesdale.

A start on the field Botany was begun shortly after arrival, when a foray was made in the vicinity of Winch Bridge, a mile or so below the hotel. Thanks to the guidance of Dr. George Taylor of the British Museum, the party were able to see some of the Teesdale rarities within a small compass. The river at Winch Bridge makes two pretty falls and then enters a narrow channel between perpendicular walls of basalt. These are draped and festooned with vegetation, and, with a fringe of woodland that comes to the edge of the gorge, form a most picturesque river scene; so that it is not surprising to learn that the place ranks as one of the beauty spots of Yorkshire. The plants noted make a formidable list, but mention may be made of the following: *Thlaspi alpestre* L., *Potentilla fruticosa* L.—both of these in crannies in the basalt—while overhead a fine specimen of *Sorbus rupicola* Sime grows and spreads its foliage towards the stream. *Arenaria verna* L. was abundant, as was *Primula farinosa* L. Most of the flowers of the latter were gone, but sufficient remained to indicate how fine a sight this plant must be at its best. Other plants noticed beside the bridge were *Juncus alpino-articulatus* Chaix and *Juncus lamprocarpus* Ehrh. growing in boggy peat near the island on which is the only known English habitat for *Melampyrum sylvaticum* L., a plant more widely distributed, though local, in Scotland.

The following day, with a grey sky overhead, the party were early astir and cars were requisitioned to furnish transport for part of the way. The objective was Widdybankfell and the route followed the Alston Road to Langdon Beck, where a rough track was struck which eventually led to a point about

Western slope of Widdybankfell, N.W. Yorks. Party searching for *Viola arenaria* at the only known British Station for this plant.

1500 feet up on the shoulder of the hill. Before proceeding very far quite a long pause was made beside the junction of the Langdon and Harwood Becks, where three interesting finds were noted—*Peucedanum Ostruthium* Koch, *Stachys officinalis* Trev. on the bank, and on the gravel of the stream *Equisetum variegatum* Schleich. A few yards farther on the Club halted to read an important notice posted beside the gate that bars the way to Widdybankfell, which reads thus—

> "NOTICE.—Owing to indiscriminate picking of flowers, several species peculiar to Teesdale are in danger of extinction. It has therefore become necessary to prohibit the picking of all flowers, and anyone picking, digging up, or otherwise destroying any flowers, ferns, or plants will be prosecuted. Raby Estate Office, 2nd May 1934."

The proprietor, Lord Barnard, has been responsible for this, one of the first applications of the new bye-laws which empower County Councils to take measures for flower protection. Watchers also patrol the area, and it was learned there had already been a prosecution. Beyond the gate an intensive search for *Gentiana verna* L. was made, but only two minute seedling plants were seen; *Kobresia caricina* Willd., however, was not uncommon. A wide moorland was then crossed towards the Tees on the Durham side opposite Cronkley Scar. Here, especially on the eastern bank of the stream, was a great display of wild flowers. *Stachys betonica* Benth. and *Bartsia alpina* L. were among the most numerous, and were in splendid condition. It was somewhat surprising to find such species together at an elevation of about 1000 feet.

Proceeding by car up the old lead miners' road the party eventually came to a point where it was necessary to proceed on foot. The route then led in the direction of the Cauldron Snout. After about a mile the path was left, and passing a rough stretch of Calluna-moor, a very interesting plant association was visited. Here, on Sugar-Limestone, grows the rare *Viola arenaria*, but considerable difficulty was experienced in finding the plant, which was in fruit. During the return to the cars the muddy slope of Widdybankfell was crossed, where on open patches of muddy sand studded with limestone fragments, its only known British habitat, was found the rare *Arenaria uliginosa*. Besides these unique Teesdale plants

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Primula farinosa and *Arenaria verna* were seen, both in quantity. Other interesting plants noted are given in the list at the end.

Sunshine and warmth ushered in the next day, when a further hill programme was undertaken. Commencing by a descent to the River Tees and crossing a farm bridge near the hotel, a direct route was taken for the habitat of *Potentilla fruticosa* L. The plant was in the finest flower and in surprising abundance. The area where it was best lay in shingle and gravel apparently liable to flooding. The plants were aged specimens, and occupied at intervals about 50 yards of the flood zone. The Yorkshire bank of the river was then followed to the beautiful gorge at High Force. Here many additional plants were flourishing, and another splendid group of *Potentilla fruticosa* adorned a good stretch high above flood level. After admiring the beauty of the river gorge a gradual approach was made to Cronkley Fell, still keeping to the west side of the river. Again an old miners' track assisted the ascent, which is somewhat steep. Near the highest point of the path, on a stretch of the same Sugar-Limestone, the first plants were seen of *Helianthemum canum* Dun. They were very stunted, and grew in association with *H. Chamaecistus* Mill, which was the commoner of the two species. A further half mile brought the party to another outcrop of Sugar-Limestone, where intermingled with both species of *Helianthemum* a growth form of *Dryas octopetala* formed a mat of hard wiry shoots with tiny foliage. It was growing under the most arid conditions, and was utterly different from the luxuriant plant of the highland hills.

The same evening quite a long time was spent in the grounds of High Force, where the rare *Poa Parnellii* was picked. In addition to this, a quick journey was made to the head of the East Grain Burn, a small watercourse that drains to the River Wear in Wensleydale, near St. John's Chapel. It had been reported that *Saxifraga Hirculus* had been collected there. The search, however, got slight reward, *Saxifraga stellaris* being the only plant seen growing over the likely sites.

The next day being Sunday an off day was called, and while no set excursion was planned most of the party went to Barnard Castle, and later made their way to Richmond, where a visit was paid to the garden of the Hon. Mr. James at St.

Potentilla fruticosa. A splendid wild specimen growing on a flood bank composed of gravel and stones. Alongside River Tees near High Force.

Robert Moyes Adam.

Nicholas. A most fascinating time was spent, for the garden has an exceptionally fine collection of recently introduced plants. Many fine things introduced by Mr. Clarence Elliott and Mr. Harold Comber were seen besides some of those introduced by the late Reginald Farrer. Some very fine species of *Lilium* were noted—*Humboldtii* from America, *Brownii* from Nepal, *Farreri* with white flowers from China, and the dark maroon-flowered *Martagon* var. *Cattaniae* called forth much admiration. On the walls of the garden was a galaxy of exotic shrubs. Among them *Mutisia decurrens* and *Mutisia retusa* (a Comber plant) were in splendid flower.

On the morrow the course was set for Baldersdale, a valley which runs parallel to the Tees at High Force. After 10 miles in the cars a long trek was begun with the object of locating the elusive *Saxifraga Hirculus*. The junction of the Lune and the Balder has been a well-authenticated locality, but for all the zeal and determination expended the plant was not found. The march took the Club over a very wide and uninteresting moorland, intersected by small streams. Peat and grass moor predominated everywhere, and only over a few isolated places at the upper end of the Balder was any likely ground noted. The search finally was abandoned and the party divided. One proceeded to Wensleydale and the other to Richmond, where interest in the river and the old Castle compensated for rather a blank day. The following morning the official programme ended, and parties went their separate ways with the feeling that another most interesting piece of country had been seen and its botanical wealth explored.

The following are some of the notable species and varieties seen with their respective locality:—

At High Force: *Betula pubescens* Ehrh., *Juniperus sibirica* Burgsdorf, and *Lastraea Filix-mas* Presl var. *abbreviata* Bab.

At Langdon Beck: *Stellaria uliginosa* Murr., *Peucedanum Ostruthium* Koch, *Stachys officinalis* Trev., and *Equisetum variegatum* Schleich.

At Winch Bridge: *Draba incana* Linn., *Thlaspi alpestre* Linn., *Rubus saxatilis* Linn., *Potentilla fruticosa* Linn., *Sorbus rupicola* Hedl., *Serratula tinctoria* Linn., *Hieracium anglicum* Fr., *Primula farinosa* Linn., *Melampyrum sylvaticum* Linn., *Salix phylicifolia* Linn., *Melica nutans* Linn., and *Juncus alpino-articulatus* Chaix (*J. alpinus* auct. angl. non Vill.).

At Widdybankfell: *Thalictrum alpinum* Linn., *Ranunculus Flammula* Linn. var. *radicans* Nolte, *Draba incana* Linn., *Viola rupestris* Schmidt var. *arenaria* Beck., *Arenaria verna* Linn., *Arenaria uliginosa* Schleich., *Poterium Sanguisorba* Linn., *Sedum villosum* Linn., *Valeriana dioica* Linn., *Oxycoccus palustris* Pers., *Gentiana verna* Linn., *Bartsia alpina* Linn., *Plantago maritima* Linn., *Tofieldia palustris* Huds., *Kobresia caricina* Willd., *Scirpus pauciflorus* Lightf., and *Botrychium Lunaria* Sw.

At Cronkley Fell: *Helianthemum canum* Baumg. and *Dryas octopetala* Linn.

A. *Arenaria uliginosum*. Plant with partially withered flowers, growing on muddy substratum western slopes of Widdybankfell.

B. *Primula farinosa*. Group of typical flowering plants, growing on wet ledges of rocky bank above River Tees at Winch Bridge, Upper Teesdale.

An Abnormal Gentian Flower.

By M. Y. Orr.

(Read 17th October 1935.)

It sometimes happens in flower morphology that the floral axis becomes extended beyond its normal limits and forms the stalk of an accessory flower of adventitious origin, which may be raised considerably above the level of the original, proliferous flower. This type of proliferation is by no means uncommon in certain genera, *Geum* for example, and in such cases the results of exuberant growth are both outward and visible.

At other times, but more infrequently and therefore of greater interest to the teratologist, the continued growth of the axis may be retarded, and the evidences of proliferation are then concealed within the central organs of the flower. This latter type of proliferation, which has been termed intra-carpellary, may be revealed only by chance dissections of the flower, since in this case the adventitious structures that may have arisen from the apex of the floral axis are dwarfed in size and are completely enveloped by the ovarian wall. Only rarely do they become so much enlarged by subsequent growth that they break through the wall and make their presence known.

Several interesting cases of intra-carpellary proliferation—mainly in Crucifers—are recorded by Masters in his *Vegetable Teratology*, while a further example of this phenomenon, discovered by the writer also in a member of the Cruciferae, has been described in an earlier number of these *Transactions*. Another instance of this particular form of abnormality was brought to the notice of the writer recently by Mr. D. Wilkie of the Royal Botanic Garden. Although similar in essence to those previously described, it differs from them in detail, and because of this and of the comparative rarity of such cases it deserves to be described.

The flower in question is a Gentian of hybrid origin, *Gentiana Waltonii* × *septemfida*, which was sent to Mr. Wilkie by a

horticulturist in Tunbridge Wells. This hybrid Gentian is said never to have set seed, and when the flower was dissected it was discovered that *within* the ovary, which in this genus is unilocular, there was another and smaller ovary, surmounted by style and stigmas, and filled with undeveloped seeds. This internal gynaeceum was attached to the base of the enveloping ovary, and evidently had arisen adventitiously from the apical region of the floral axis. The appearance presented by this abnormal flower after dissection is shown in the text-figure.

FIG. 1.—Vertical section of a flower of *Gentiana Waltonii* × *septemfida*, showing the internal gynaeceum (outlined in black) in the centre.
(Del. B. G. Watts.)

In one of the cases of intra-carpellary proliferation figured by Masters a miniature replica of a normal fruit of the Wall-flower is shown attached to the inner wall of a siliqua. Masters states that there was no indication of floral envelopes, the adventitious flower in this case being represented solely by ripened carpels. It would seem that a parallel case is presented by the flower of the Gentian, and the production of an ovary within an ovary in the latter is to be regarded therefore as the outcome of abortive intra-carpellary proliferation of the flower.

REFERENCES.

MASTERS, M. T.: Vegetable Teratology, London, 1869, pp. 132, 181, 182.
ORR, M. Y.: Trans. Bot. Soc. Edin., xxix (1924), 10.

OBITUARY NOTICE.

Robert Alexander Robertson.

Born at Rattray, Perthshire, in 1873, R. A. Robertson was a graduate in Arts and in Science of the University of Edinburgh. He became assistant under Professor W. C. M'Intosh at St. Andrews in 1889. In 1891 he was appointed Lecturer in Botany, his status being raised to that of Reader in 1915. A Chair of Botany in the University was founded in 1929, and Professor Robertson became its first occupant. He retired in September 1934 and passed away in January 1935.

Robertson was a great teacher both in the class room and in the research field. Labouring incessantly to keep himself proficient, he had the power of imparting knowledge, developing initiative, and creating enthusiasm. The published record of research by himself and by the Botany school at St. Andrews covers varied fields. The application of photomicrography to opaque objects was pioneer work in the closing years of last century. This paved the way to contributions on the histology of fossil woods and to the preparation of an atlas dealing with the micro-identification of timbers. The atlas was never published, but several of the plates were exhibited at the Royal Society, Burlington House. The application of histology as an aid to taxonomy is illustrated by his paper on *Potentilla*. Other histological publications deal with plant pathology, abnormal conjugation in *Spirogyra*, and variations in *Lycopodium clavatum* with their bearing on phylogeny. Work on *Osmunda* and on *Isoetes* was unfortunately unpublished.

In 1901–1904 appeared a series of publications advocating the then new conception of functional inertia by examples drawn from the vegetable kingdom. As president of the Scottish Microscopical Society in 1906 he chose Osmosis as the subject of his address.

In 1908 publications dealing with sense organs in plants appeared, with records of ocelli in the stems of plants. Studies in growth and in transpiration in the succeeding years lead up to the publication of *Plant Growth Rhythms* in 1913.

At the outbreak of the World War, Robertson was Captain

of the St. Andrews O.T.C. He was an enthusiast for military training, and for his services during the crisis his name will ever remain green.

Following the War there issued from St. Andrews Botany school an interesting series of contributions on the maritime flora of Fife, particularly the strand and the salt marsh plants. These papers were interspersed with histological, mycological, and physiological contributions. The flow of publications continued under the names of the individual investigators, Robertson scorning to countenance joint authorship, and these show an active participation in research work until his retirement.

Professor Robertson, who was elected a Fellow of the Botanical Society of Edinburgh in 1890, became its President in 1915. He was elected a Fellow of the Royal Society of Edinburgh in 1902, and of the Linnean Society in 1903. He was elected to the Honorary Committee of Management of the Imperial Bureau of Mycology from its inception in 1922.

A man of wide sympathy and with the gift of humour, a man of high principle, steadfast in his loyalty to justice and honour, a man above subterfuge, he devoted a life to the advancement of botany in Scotland. His death within four months of his retirement from the Chair of Botany in the University of St. Andrews came as a blow to his friends who had hoped for his company, and an irreparable loss to those who loved him best.

R. J. D. G.

ROLL

OF

THE BOTANICAL SOCIETY OF EDINBURGH.

Corrected to 1st November 1935.

Patron:

HIS MOST GRACIOUS MAJESTY THE KING.

HONORARY FELLOWS.

BRITISH SUBJECTS (LIMITED TO TWELVE).

Date of Election.

Dec. 1907. FARMER, Sir JOHN BRETLAND, M.A., D.Sc., F.R.S., *Emeritus Professor, Imperial College of Science and Technology, South Kensington, St. Leonard's, Weston Road, Bath.*

Dec. 1930. LANG, WILLIAM HENRY, M.B., C.M., D.Sc., F.R.S., *Barker Professor of Cryptogamic Botany, University of Manchester.*

April 1935. LLOYD, FRANCIS ERNEST, M.A., D.Sc., F.L.S., *late Macdonald Professor of Botany, M'Gill University, Montreal, Canada.*

June 1923. PRAEGER, ROBERT LLOYD, B.A., D.Sc., 19 *Fitzwilliam Square, Dublin.*

June 1923. RENDLE, ALFRED BARTON, M.A., D.Sc., F.R.S., "*Talland,*" *The Mount, Fetcham Park, Leatherhead, Surrey.*

April 1935. SEWARD, ALBERT CHARLES, M.A., Sc.D., F.R.S., *Professor of Botany in the University of Cambridge, The Lodge, Downing College, Cambridge.*

FOREIGN (LIMITED TO TWENTY-FIVE).

June 1923. CAMPBELL, Dr. DOUGLAS HOUGHTON, *Professor of Botany, Stanford University, California;—Corresponding Member, Dec.* 1905.

Oct. 1935. CLAUSEN, Dr. JENS, *Carnegie Institution of Washington, Division of Plant Biology, Stanford University, California.*

Mar. 1934. DIELS, LUDWIG, Dr. Phil., F.L.S., *Professor of Botany and Director of the Botanic Garden and Museum, Berlin-Dahlem.*

Oct. 1935. ELFVING, Dr. FREDRIK, *Professor Emeritus of Botany, Köpmansgatan* 10, *Helsingfors, Finland;—Corresponding Member, Mar.* 1895.

Mar. 1934. HANDEL-MAZZETTI, Dr. HEINRICH, *Botanische Institut der Universität, Rennweg* 14, *Wien III, Austria.*

Date of Election.

June 1923. IKENO, Professor SEITTSIRO, Ph.D., *Agricultural College, Imperial University, Tokyo, Japan.*

June 1923. MACDOUGALL, Dr. D. T., *Director of Department of Botanical Research, Carnegie Institution, Tucson, Arizona, U.S.A.*

Oct. 1935. MIYABE, Dr. KINGO, *Emeritus Professor of Botany, Hokkaido Imperial University, Sapporo, Hokkaido, Japan;—Corresponding Member, Dec.* 1905.

Oct. 1935. MIYOSHI, Dr. MANABU, *Professor Emeritus of the Imperial University, Hongo, Tokyo, Japan;—Corresponding Member, June* 1902.

June 1923. OSTERHOUT, W. J. V., Ph.D., *Rockefeller Institute, 66th Street and Avenue A, New York, U.S.A.*

Oct. 1935. RAUNKIAER, Professor CHRISTEN, *Botaniske Museum, Copenhagen, Denmark;—Corresponding Member, June* 1902.

Mar. 1934. REHDER, ALFRED, A. M., *Curator, Arnold Arboretum, Jamaica Plain, Mass., U.S.A.*

June 1902. TRELEASE, Dr. WILLIAM, *University of Illinois, Urbana, Illinois, U.S.A.*

Mar. 1934. TUBEUF, CARL FREIHERR VON, Professor Dr., *Habsburger Str.* 1. *Munich, Germany.*

Mar. 1934. TURESSON, G. W., Fil.Dr., *The University, Lund, Sweden.*

Mar. 1934. VAVILOV, Professor N. I., *Director of the State Institute for Experimental Agronomy, Ul. Gerzena, Leningrad, U.S.S.R.*

Oct. 1935. WESTERDIJK, Dr. JOH., *Professor of Phytopathology Utrecht and Amsterdam, Javalaan,* 4, *Baarn, Holland.*

ORDINARY FELLOWS.

No distinguishing mark is placed before the name of Fellows who contribute annually and receive Publications.

** Indicates Fellows who have compounded for Annual Contribution and receive Publications.*

† Indicates Non-Resident Fellows who have compounded for Publications.

‡ Indicates Non-Resident Fellows who do not receive Publications.

Date of Election.

Dec. 1915. Adam, Robert Moyes, F.L.S., 17 *West Brighton Crescent, Portobello, Edinburgh.*

Jan. 1934. Ainsworth, Sir T., Bart., *Ardanaiseig, Kilchrenan, Argyll.*

Jan. 1924. Aitken, Mrs. W., 54 *Braid Road, Edinburgh,* 10.

Nov. 1924. *Alcock, Mrs. N. L., M.B.E., F.L.S., 14 *Inverleith Row, Edinburgh,* 4.

Feb. 1925 Anderson, J. B., 76 *South Trinity Road, Edinburgh,* 5.

Nov. 1926. *Anthony, John, M.C., M.A., B.Sc., 7 *Craigcrook Gardens, Edinburgh,* 4.

Dec. 1924. Armstrong, D., *The Drum, Gilmerton, Midlothian.*

Dec. 1908. ‡Balfour, F. R. S., M.A., 13 *Collingham Gardens, London, S.W.* 5.

Oct. 1935. Barr, Rev. Robt., M.A., J.P., *The Manse, Neilston, Renfrewshire.*

May 1891. *Berwick, Thomas, 56 *North Street, St. Andrews.*

Feb. 1919. †Blackburne, Cecil Ireland, *Weydown Hatch, Haslemere, Surrey.*

April 1926. Blackie, John Joseph, Ph.D., A.I.C., Ph.C., 104 *Holyrood Road, Edinburgh,* 8.

May 1888. *Bonnar, William, 51 *Braid Avenue, Edinburgh,* 10.

Jan. 1899. *Borthwick, A. W., O.B.E., D.Sc., *Professor of Forestry, The University, Aberdeen.*

Oct. 1935. Bowden, John, B.Sc., 55 *March Road, Blackhall, Edinburgh,* 4.

Dec. 1886. *Bower, F. O., M.A., D.Sc., F.R.S., F.L.S., 2 *The Crescent, Ripon.*

Mar. 1927. Boyd, Miss Lucy, D.Sc., 3 *West Brighton Crescent, Portobello, Edinburgh.*

Oct. 1935. Braid, Professor K. W., M.A., B.Sc., 6 *Blythswood Square, Glasgow.*

May 1924. †Brown, Miss Helen M., *Longformacus, Duns.*

Dec. 1906. †Bryce, George, D.Sc., *Dept. of Agriculture, Ibadan, Nigeria.*

April 1926. Buchan, The Right Hon. the Earl of, *Almondell House, Mid-Calder.*

Nov. 1922. Buchanan, E. M., 76 *Warrender Park Road, Edinburgh,* 10.

Dec. 1921. ‡Burns, W., D.Sc.

Oct. 1928. Burrell, Sir William, *Hutton Castle, Berwick-on-Tweed.*

Dec. 1924. †Burt, Miss C. C., B.Sc., 36 *Ravenshaugh Road, Levenhall, Musselburgh.*

Date of Election.

Oct. 1926. *Callender, Wm. C., *Georgefield*, 31 *Inverleith Terrace, Edinburgh*, 4.
Oct. 1925. Campbell, Mrs. Agnes, *Aros, Colinton.*
Jan. 1935. Chen, Feng-hwai, *Royal Botanic Garden, Edinburgh*, 4.
Dec. 1928. Clarke, Robert R., B.Sc., *Whitehall, Aberdour, Fife.*
Feb. 1933. Clouston, David, C.I.E., M.A., D.Sc., *Forthview, Boswall Road, Edinburgh*, 5.
Oct. 1935. Coates, Henry, *Kydal, Wheatridge Lane, Torquay.*
April 1913. ‡Cooper, R. E., *Royal Botanic Garden, Edinburgh*, 4.
Nov. 1932. Corstorphine, R. H., *Inchdowrie, Glen Clova, Angus.*
Mar. 1900. *Cowan, Alexander, *Valleyfield, Penicuik.*
Nov. 1933. Cowan, C. M., *St. Michaels, Musselburgh.*
Oct. 1930. Cowan, John M., M.A., D.Sc., 17 *Inverleith Place, Edinburgh*, 4.
June 1929. Cowan, Robert Craig, *Lochside Cottage, Duddingston, Edinburgh.*
Feb. 1923. †Cox, E. H. M., 2 *Stafford Street, Old Bond Street, London, W.* 1.
Jan. 1922. *Dales, Mrs. H., M.A., B.Sc., *Allora, Kensington Gardens, Knock, Belfast.*
Oct. 1926. Davey, V. E. M., B.Sc., Ph.D., *Plant Breeding Station, Corstorphine, Edinburgh*, 12.
Dec. 1903. Davidson, J. Randolph, M.A., B.Sc., 25 *Meadway Court, Golders Green, London, N.W.* 11.
Dec. 1911. ‡Davidson, John, F.L.S., *Associate Professor of Botany, University of British Columbia, Vancouver, Canada.*
Nov. 1925. De Pree, Mrs., *Beach Hill, Haddington.*
Dec. 1930. Dickson, Miss A. M., *Woodhouse, Dunscore, Dumfriesshire.*
Nov. 1927. *Dobson, Miss Margaret Gairns, 8 *Polwarth Terrace, Edinburgh*, 11.
Nov. 1919. *Downie, Miss D. G., B.Sc., 1 *W. Stanhope Place, Edinburgh*, 12.
Feb. 1931. Egerton, Major-General Granville, 7 *Inverleith Place, Edinburgh*, 4.
Feb. 1917. †Eley, Charles, *East Bergholt Place, Suffolk.*
Mar. 1932. Elphinstone, The Right Hon. Lady, *Carberry Tower, Musselburgh.*
Jan. 1883. *Evans, Arthur H., Sc.D., *Cheviot House, Crowthorne, Berks.*
Dec. 1905. *Evans, W. Edgar, B.Sc., F.R.S.E., 38 *Morningside Park, Edinburgh*, 10.
Jan. 1935. Fang, Wen Pei, *Royal Botanic Garden, Edinburgh*, 4.
Dec. 1927. Fenton, E. Wyllie, M.A., B.Sc., F.L.S., 16 *Wilton Road, Edinburgh*, 9.
Dec. 1933. Fleming, Mrs. E. M., 10 *Chester Street, Edinburgh*, 3.
Oct. 1934. Fleming, G. J., 30 *Royal Circus, Edinburgh*, 3.
Dec. 1934. Fletcher, H. R., B.Sc., Ph.D., *Royal Botanic Garden, Edinburgh*, 4.
Oct. 1928. Foister, Charles Edward, B.A., Ph.D., c/o Hodgkinson, 15 *Goldenacre Terrace, Edinburgh*, 4.
Dec. 1931. Forrest, Miss Grace, 11 *Rothesay Place, Edinburgh*, 3.
Feb. 1931. Fortune, T. A. S., *Cairngreen, Davidson's Mains, Edinburgh*, 4.
Jan. 1906. *Fraser, James, 18 *Park Road, Edinburgh*, 6.
Oct. 1920. *Galloway, R. Angus, M.C., B.Sc., 65 *Cluny Gardens, Edinburgh*, 10.
Dec. 1920. †Garriock, John, M.A., B.Sc., *Morgan Academy, Dundee.*
Feb. 1933. Gemmell, James W. S., M.A., B.Sc., 74 *Victoria Terrace, Dunfermline.*
May 1903. ‡Gilmore, Dr. Owen, L.R.C.P., L.R.C.S.E., 49 *Acre Lane, Brixton, London, S.W.* 2.
Dec. 1907. Gourlay, Dr. W. Balfour, M.C., 7 *Millington Road, Cambridge.*
Nov. 1921. *Graham, R. J. D., M.A., D.Sc., *Professor of Botany, The University, St. Andrews.*
Mar. 1923. Gray, John H., M.A., B.Sc., 28 *West Relugas Road, Edinburgh*, 9.
Jan. 1926. Gregor, James W., Ph.D., F.L.S., *North Clermiston House, Cramond Bridge.*
Mar. 1925. *Grieve, Miss Jean E., 11 *Lauder Road, Edinburgh*, 9.
Oct. 1935. Gwynne-Vaughan, Dame Helen, G.B.E., LL.D., 93 *Bedfort Court Mansions, London, W.C.* 1.
Nov. 1932. Hales, Mrs. Jessie B., 48 *Craiglockhart Road, Edinburgh*, 11.
Nov. 1914. †Harley, Andrew, *Blinkbonny, Kirkcaldy.*
Dec. 1923. †Harris, Mrs. K., B.Sc., *Oakleigh, Elm Road, Early, Reading.*
April 1910. Harvey, Miss Elsie, *Kerala, Captain's Road, Liberton, Edinburgh*, 9.
Mar. 1913. †Hayward, Miss Ida M., F.L.S., 7 *Abbotsford Road, Galashiels.*
Dec. 1929. Heddle, R. G., M.A., B.Sc., 13 *George Square, Edinburgh*, 8.
May 1924. ‡Henderson, George, *Royal Academy, Inverness.*
April 1886. Hill, J. Rutherford, Ph.C., *Secretary, Pharmaceutical Society*, 36 *York Place, Edinburgh*, 1.
Oct. 1926. †Home, Miss Logan, *Edrom House, Edrom, Berwickshire.*
Mar. 1920. Howison, Andrew, M.A., B.Sc., 18 *Beresford Avenue, Edinburgh*, 5.

Date of Election.	
Jan. 1935.	Jardine, Brig.-Gen. J. B., C.M.G., D.S.O., *Chesterknowes, by Selkirk.*
Oct. 1931.	Jeffers, R. H., N.D.H., F.C.S., 42 *Archevy Road, Eltham, London, S.E.* 9.
Dec. 1907.	*Jeffrey, J. Frederick, *Laneside, Shipham, Winscombe, Somerset.*
May 1877.	*Johnston, Henry Halcro, C.B., C.B.E., D.Sc., M.D., F.L.S., Colonel R.A.M.C., c/o Miss J. Grant, 32 *Dundas Crescent, Kirkwall, Orkney.*
Dec. 1912.	*Johnstone, James Todd, M.A., B.Sc., *Royal Botanic Garden, Edinburgh*, 4.
Jan. 1913.	*Kemp, Mrs. C Norman, M.A., D.Sc., *Ivy Lodge, Laverockbank Road, Edinburgh*, 5.
Nov. 1924.	*King, Miss C. A., *Osborne Nursery, Corstorphine Road, Edinburgh*, 12.
Oct. 1921.	King, Miss Isabella M., B.Sc., 4 *Cambridge Gardens, Edinburgh*, 6.
Jan. 1932.	Knott, Eric, Ph.C., 72 *Craigleith Road, Edinburgh*, 4.
Jan. 1924.	*Knox, Mrs. J., M.A., B.Sc., 43 *Dalhousie Terrace, Edinburgh*, 10.
Nov. 1921.	*Laing, Ernest V., M.A., D.Sc., 13 *Belvedere Street, Aberdeen.*
Oct. 1935.	Lamb, Ivan M., B.Sc., *Dept. of Botany, British Museum (Natural History), Cromwell Road, London, S.W.* 7.
Dec. 1911.	*Lamont, Miss Augusta, M.A., B.Sc., *Inverchaolain, Toward, Argyllshire.*
Oct. 1934.	Landale, S. E. A., Ph.D., *Ellersly, Murrayfield, Edinburgh*, 12.
Nov. 1927.	Lang, J. M. S., B.S.A., *Craig's House, Corstorphine, Edinburgh*, 12.
May 1931.	Latham, H. A., 27 *Oxgangs Road, Lothianburn, Edinburgh.*
Oct. 1935.	Lauder, Thomas, 218 *Parliamentary Road, Glasgow.*
Dec. 1917.	Law, Mrs. John, 41 *Heriot Row, Edinburgh*, 3.
Dec. 1922.	*Lewis, Herbert M., B.Sc., *Penucha, Caerwys, N. Wales.*
Oct. 1925.	†Low, Wm., *Balmakewan, Marykirk, Laurencekirk.*
Nov. 1922.	‡M'Call, David, B.Sc., Ph.D., *Dundee Technical College, Bell Street, Dundee.*
Oct. 1935.	M'Cutcheon, William, B.Sc., 89 *Argyle Road, Saltcoats.*
Feb. 1925.	Macdonald, James, B.Sc., *Imperial Forestry Institute, Oxford.*
Feb. 1933.	Macdonald, James A., B.Sc., Ph.D., *Botany Dept., The University, St. Andrews.*
Jan. 1895.	MacDougall, R. Stewart, M.A., D.Sc., LL.D., *Ivy Lodge, Gullane, East Lothian.*
Jan. 1881.	†Macfarlane, John M., Sc.D., LL.D., F.R.S.E., *Emeritus-Professor of Botany*, 427 *West Hansberry Street, Germantown, Pa., U.S.A.*
Dec. 1925.	*M'Intosh, A. E. S., B.Sc., Ph.D., *Assistant Geneticist, Dept. of Science and Agriculture, Barbados, B.W.I.*
Oct. 1935.	M'Intosh, James, *Atholl Street, Dunkeld.*
Dec. 1925.	Mackie, Miss A. W., 11 *Bellevue Terrace, Edinburgh*, 7.
Dec. 1934.	M'Rae, Wm., C.I.E., M.A., D.Sc., 189 *Newhaven Road, Edinburgh*, 6.
Feb. 1914.	Macwatt, John, M.B., C.M., *Morelands, Duns.*
Dec. 1896.	‡Mahalanobis, Professor S. C., B.Sc., F.R.S.E., P. 45 *New Park Street, Calcutta.*
Nov. 1933.	Maitland, T. D., M.B.E., 20 *Craiglockhart Terrace, Edinburgh*, 11.
Dec. 1934.	Marindin, Mrs., *Fordel, Glenfarg, Perthshire.*
Oct. 1914.	*Martin, Miss Isa, M.A., *Hillview, Aberdour Road, Dunfermline.*
April 1933.	Mather, Carroll J., Ph.C., B.S., 228 *South Gratiot Avenue, Mount Clement, Michigan, U.S.A.*
April 1933.	Mather, Enoch, M.S., M.D., 228 *South Gratiot Avenue, Mount Clement, Michigan, U.S.A.*
Mar. 1913.	*Matthews, James R., M.A., *Professor of Botany, The University, Old Aberdeen.*
Dec. 1916.	†Maxwell, Sir John Stirling, Bart., *Pollok, Pollokshaws, Glasgow.*
Nov. 1932.	Meade, Francis H., *The Hangingshaw, Selkirk.*
Oct. 1925.	Mercer, Miss Edith, 10 *Ventnor Terrace, Edinburgh*, 9.
April 1919.	‡Mills, A. E., 37 *High Street, Keynsham, near Bristol.*
Dec. 1930.	Muirhead, Charles, 22 *Learmonth Terrace, Edinburgh*, 4.
Oct. 1918.	†Murray, J. M., B.Sc., F.R.S.E., 25 *Drumsheugh Gardens, Edinburgh*, 3.
Dec. 1923.	*Nelson, Alex., B.Sc., Ph.D., *Royal Botanic Garden, Edinburgh*, 4.
April 1916.	†Nicholson, C., F.E.S., "*Nansgwithick*," *Tresillian, Truro, Cornwall.*
Dec. 1907.	*Orr, M. Y., F.R.S.E., *Royal Botanic Garden, Edinburgh*, 4.
Oct. 1914.	†Patton, Donald, M.A., B.Sc., Ph.D., 15 *Jordanhill Drive, Glasgow, W.* 3.

Date of Election.	
Nov. 1919.	Pealling, Robert J., M.A., B.Sc., *The Royal Academy, Inverness.*
Dec. 1917.	*Pike, J. Lyford, B.Sc., *Rosetta, 56 Kirkbrae, Liberton, Edinburgh, 9.*
Jan. 1915.	*Pinkerton, A. A., *Adele Cottage, Loanhead.*
June 1891.	†Prain, Sir David, M.D., C.I.E., F.R.S.S.L. & E., F.L.S., *The Well Farm, Warlingham, Surrey.*
Jan. 1932.	Pratt, Alex., B.Sc., *Vierstraat, St. Michaels, Leuchars, Fife.*
Oct. 1935.	Ramsbottom, J., O.B.E., M.A., *Natural History Museum, Cromwell Road, London, S.W. 7.*
Dec. 1932.	Redman, Miss A. W. H., B.Sc., 30 *Lomond Road, Edinburgh, 5.*
Oct. 1927.	Reid, Mrs. Murray, *Easter Belmont, Murrayfield, Edinburgh, 12.*
April 1877.	‡Riddell, Wm. R., B.A., B.Sc. (Hon. Mr. Justice), *Osgoode Hall, Toronto, Canada.*
Feb. 1926.	Robb, William, N.D.A., *Craig's House, Corstorphine, Edinburgh, 12.*
Mar. 1925.	†Rothschild, Lionel N. de, *Exbury, near Southampton.*
Dec. 1889.	‡Russell-Murray, J., 241 *Clark Avenue, Westmount, Montreal, Canada.*
Mar. 1935.	Sandilands, James, F.I.C., 102 *Westholmes Gardens, Musselburgh.*
May 1926.	‡Sangster, Mrs. Iris, *Fullerswood Park, Mountain Side P.O., Jamaica.*
Feb. 1932.	Scarlett, R. L., C.D.A., *Sweethope, Musselburgh.*
Dec. 1887.	‡Scott, J. S., L.S.A., 69 *Clowes Street, West Gorton, Manchester.*
June 1922.	†Simpson, J. R., *Longview, Eildon Street, Galashiels.*
Mar. 1925.	Smart, Mrs. J. P., *Mahaar Schoolhouse, Kirkcolm, Stranraer.*
Dec. 1922.	Smith, Miss Edith Philip, B.A., Ph.D., F.L.S., 46 *Murrayfield Avenue, Edinburgh, 12.*
Nov. 1926.	‡Smith, H. Guthrie, *Tutira, Napier, New Zealand.*
Nov. 1914.	*Smith, James L. S., M.A., B.Sc., 29 *Wardie Road, Edinburgh, 5.*
Dec. 1917.	†Smith, J. T., 68 *Tennant Street, Glasgow.*
Oct. 1935.	Smith, Rupert, 38 *Greenhill Gardens, Edinburgh, 10.*
Jan. 1902.	*Smith, Professor Sir Wm. Wright Smith, M.A., *King's Botanist, Regius Keeper, Royal Botanic Garden, Edinburgh, 4.*
Nov. 1923.	†Stern, Frederick, *Highdown, Goring-on-Sea.*
Oct. 1923.	†Stevenson, J. B., *Tower Court, Ascot.*
Oct. 1914.	†Stewart, Edward J. A., M.A., B.Sc., 8 *Manor Road, Jordanhill, Glasgow.*
April 1921.	Sutherland, Sir John, C.B.E., LL.D., 11 *Inverleith Row, Edinburgh, 4.*
May 1928.	Sutherland, Lady, 11 *Inverleith Row, Edinburgh, 4.*
Jan. 1913.	‡Tagg, M. H., 53 *Clayton Avenue, Wembley, Middlesex.*
Oct. 1926.	*Taylor, George, D.Sc., F.R.S.E., *Dept. of Botany, British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.*
Dec. 1922.	†Taylor, George Crosbie, B.Sc., F.L.S., 20 *Tavistock Street, Covent Garden, London, W.C. 2.*
Dec. 1923.	†Taylor, James, M.A., B.Sc., *High School, Dalbeattie, Kirkcudbrightshire.*
May 1923.	†Taylor, R. A., B.Sc., *Dept. of Botany, University College, Dundee.*
Oct. 1929.	Terras, Mrs. Kate R., 40 *Findhorn Place, Edinburgh, 9.*
Oct. 1932.	Tetley, Miss U., M.Sc., *Quarry Garth, Windermere, Westmoreland.*
April 1921.	†Thompson, Professor J. MacLean, M.A., D.Sc., F.L.S., *Dept. of Botany, The University, Liverpool.*
Oct. 1928.	Thomson, Miss Norah M'Nab, 30 *Drumsheugh Gardens, Edinburgh, 3.*
Dec. 1933.	Walton, H. G., C.S.I., *Springfield House, Inveresk.*
Mar. 1932.	Walton, John, M.A., D.Sc., *Professor of Botany, The University, Glasgow.*
Oct. 1918.	†Watson, Harry, *Benmore Forest School, Dunoon, Argyll.*
Mar. 1925.	*Watt, James, LL.D., W.S., 28 *Charlotte Square, Edinburgh, 2.*
April 1930.	*Watt, Mrs. Menie, 7 *Blackford Road, Edinburgh, 10.*
Nov. 1921.	Watt, Miss Janet, 2 *W. Catherine Place, Edinburgh, 12.*
Dec. 1930.	Whyte, James H., B.Sc., *Botany Dept., M'Gill University, Montreal, Canada.*
Oct. 1935.	Williamson, William, F.R.S.E., F.L.S., 47 *St. Albans Road, Edinburgh, 9.*
Dec. 1922.	Wilson, Miss Dorothy G., B.Sc., *Secondary School for Girls, 53 Parliament Street, Stockton-on-Tees.*
Feb. 1912.	*Wilson, Malcolm, D.Sc., *Brentknoll, Kinnear Road, Edinburgh, 4.*
Mar. 1909.	*Wilson, Thos., Ph.C., 110 *High Street, Burntisland.*
Jan. 1903.	Young, William, *Fairview, Kirkcaldy.*
Jan. 1923.	*Younger, Harry Geo., *Kittoes, Bishopsteignton, S. Devon.*

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Nov. 1932.	Callen, Eric O., 9 *Lauderdale Street, Edinburgh*, 10.
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Nov. 1933.	Cant, Miss Christine M., *Schoolhouse, Balbardie Road, Bathgate.*
Oct. 1935.	Clouston, David, M.A., D.Sc., *North of Scotland Agricultural College, Union Street, Aberdeen.*
Nov. 1930.	Cowan, Mrs., 17 *Inverleith Place, Edinburgh*, 4.
Oct. 1935.	Cowan, Lt.-Col. S. Hunter, D.S.O., *The New Club, Princes Street, Edinburgh*, 2.
Dec. 1934.	Cumming, Miss M. G., 18 *Scone Gardens, Edinburgh*, 8.
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Dec. 1934.	Dawson, J. L., *Maywood, Linlithgow.*
Nov. 1931.	Drummond, Ronald T., 26 *Nile Grove, Edinburgh*, 10.
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April 1925.	M'Ilvenna, Wm. R., 14 *Inverleith Place, Edinburgh*, 4.
Dec. 1931.	Macsween, James C., B.Sc., *Craigstone, Ratho, Edinburgh.*
Nov. 1931.	Murray, Charles, B.Sc., *Kirkcaldy High School, Kirkcaldy.*
Nov. 1928.	Murray, John, B.Sc., *Whitslade, Broughton, Peeblesshire.*
Oct. 1932.	Noble, Miss Mary, B.Sc., Ph.D., 19A *Willowbrae Avenue, Edinburgh*, 8.
Nov. 1931.	Orr, Henry R., B.Sc., *Botanical Dept., The University, Aberdeen.*
Mar. 1935.	Parker, W. A., D.S.O., J.P., M.Inst.C.E., 10 *Dean Park Crescent, Edinburgh*, 4.
Feb. 1928.	Pearson, Miss Peggy, *Otterburn, Kelso.*
April 1925.	Robertson, Mrs. Marjory F., 23 *Inverleith Place, Edinburgh*, 4.
April 1930.	Robson, Thomas, 6 *Kirkhill Road, Edinburgh*, 9.
Nov. 1931.	Russell, James R., B.Sc., 304 *Morningside Road, Edinburgh*, 10.
Dec. 1933.	Scott, R. A., B.Sc., Ph.D., *Dept. of Agriculture, Launceston, Tasmania.*
Dec. 1933.	Scott, Wm. J. Sage, B.Sc., 4 *Greenhill Terrace, Edinburgh*, 10.
Nov. 1931.	Shearer, Miss Winifred, B.Sc., 1 *Rugby Road, Newport, Mon.*
Nov. 1932.	Sinclair, James, c/o Mrs. Kidd, 282 *Easter Road, Edinburgh*, 6.
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Oct. 1927.	Stevenson, Miss J. J., 7 *South Trinity Road, Edinburgh*, 5.
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Dec. 1930.	Torbock, H. C., *Crossing Hall, Cliburn, Penrith.*
Dec. 1923.	Wallace, G. B., B.Sc., Ph.D., 19 *Joppa Road, Portobello, Edinburgh.*
Nov. 1931.	Waterston, John M., B.Sc., 113 *Marchmont Road, Edinburgh*, 10.
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Nov. 1928.	Wilson, A. R., M.Sc., *North Clermiston House, Barnton, Mid-Lothian.*

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Jan. 1906. Harrow, R. L., *Director, Royal Horticultural Society's Gardens, Wisley, Ripley, Surrey.*

Feb. 1919. Johnson, Norman M., B.Sc., *Ardgarth, Victoria Terrace, Dunfermline.*

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April 1893. Balfour, Lady Bayley, *Penfold's Corner, Haslemere, Surrey.*

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Nov. 1926. Smith, Lady, *Inverleith House, Edinburgh,* 4.

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Dec. 1905. Mattirolo, Professor O., *R. Istituto Botanico, Torino* (120) *Italy.*

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Svenska Botaniska Föreningen.
Upsala, ... Kungl. Vetenskaps Societeten.
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Institut Botanique, Herbier Boissier.
Zurich, ... Naturforschende Gesellschaft.
Schweizerische botanische Gesellschaft.

AFRICA.

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Pusa, ... Agricultural Research Station.
Peradeniya, . . Royal Botanic Gardens.
Singapore, . . . Botanic Gardens.
Manila, ... Bureau of Science.
Buitenzorg, . . . Departement van Landbouw, Nijverheid en Handel.
Shanghai, . . . Science Society of China.
Formosa, . . . Department of Forestry, Government Research Institute, Taihoku Imperial University.
Kurashiki, . . . Ohara Institute for Agricultural Research.
Sapporo, . . . Sapporo Natural History Society.
Sendai, ... Biological Institute, Tohoku Imperial University.
Tokio, ... College of Agriculture, Imperial University.

AUSTRALASIA.

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Royal Society of Queensland.
Hobart, ... Royal Society of Tasmania.
Launceston, . . Department of Agriculture, Tasmania.
Melbourne, . . . Botanical Department, University of Melbourne.
National Herbarium.
Royal Society of Victoria.
Sydney, ... Fisher Library, Sydney University.
Linnean Society of New South Wales.
Royal Society of New South Wales.
Wellington, . . . Royal Society of New Zealand.

CANADA.

Halifax, ... Nova Scotian Institute of Natural Science.
Montreal, . . . M'Gill University.
Ottawa, ... Canadian Forestry Association.
Central Experiment Farms.
Department of Agriculture.
Department of the Interior, Forestry Branch.
Geological Survey of Canada.
Toronto, ... Royal Canadian Institute.

SOUTH AMERICA.

Bogota, ... Ministry of Public Works.
Buenos Aires, . . Museo Naçional de Historia Natural.
La Plata, . . . Museo de La Plata.
Monte Video, . . Museo Naçional de Monte Video.
Rio de Janeiro, . Instituto de Biologia Vegetal.
Museu Naçional.
San Paulo, . . Secção de Botanica e Agronomia.

UNITED STATES.

Ames, Iowa, . . Iowa State College.
Ann Arbor, Mich., University of Michigan.
Berkeley, Cal., . University of California.
Boston, Mass., . Society of Natural History.
Brooklyn, N.Y., . Brooklyn Botanic Garden.
Cambridge, Mass., Gray Herbarium, Harvard University.
Cincinnati, O., . Lloyd Botanical Library.
Society of Natural History.
Colorado Springs, Col., Colorado College.
Columbia, Mo., . University of Missouri.
Columbus, O., . Ohio State University.
Geneva, N.Y., . . Agricultural Experiment Station.
Indianapolis, Ind., Indiana Academy of Sciences.
Ithaca, N.Y., . . New York State College of Agriculture.
Jamaica Plain, Mass., Arnold Arboretum.
La Fayette, Ind., . Purdue University Agricultural Experiment Station.
Lawrence, Kan., . Kansas Academy of Science.
Madison, Wis., . Agricultural Experiment Station.
Wisconsin Academy of Sciences.
Manhattan, Kan., State Agricultural College.

Milwaukee, Wis.,	Public Museum.
Minneapolis, Minn.,	Botanical Department, University of Minnesota.
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New York, N. Y.,	Academy of Sciences.
	Torrey Botanical Club.
Philadelphia, Pa.,	Academy of Natural Sciences.
	American Philosophical Society.
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St. Louis, Mo.,	Missouri Botanical Garden.
San Francisco, Cal.,	California Academy of Sciences.
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Urbana, Ill.,	University of Illinois.
Washington, D.C.,	National Academy of Sciences.
	Smithsonian Institution.
	United States Department of Agriculture; Forest Service; National Museum; Office of Experiment Stations.
Woods Hole, Mass.,	Marine Biological Laboratory.

WEST INDIES.

Jamaica,	Department of Agriculture.
Trinidad,	Royal Botanic Garden.

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